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REVIEW

A review of Southern Ocean squids using nets and beaks

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Abstract

This review presents an innovative approach to investigate the teuthofauna from the Southern Ocean by combining two complementary data sets, the literature on cephalopod taxonomy and biogeography, together with predator dietary investigations. Sixty squids were recorded south of the Subtropical Front, including one circumpolar Antarctic (*Psychroteuthis glacialis* Thiele, 1920), 13 circumpolar Southern Ocean, 20 circumpolar subantarctic, eight regional subantarctic, and 12 occasional subantarctic species. A critical evaluation removed five species from the list, and one species has an unknown taxonomic status. The 42 Southern Ocean squids belong to three large taxonomic units, bathyteuthoids ($n = 1$ species), myopsids ($n = 1$), and oegopsids ($n = 40$). A high level of endemism (21 species, 50%, all oegopsids) characterizes the Southern Ocean teuthofauna. Seventeen families of oegopsids are represented, with three dominating families, onychoteuthids (seven species, five endemics), ommastrephids (six species, three endemics), and cranchiids (five species, three endemics). Recent improvements in beak identification and taxonomy allowed making new correspondence between beak and species names, such as *Galiteuthis suhmi* (Hoyle 1886), *Liguriella podophtalma* Issel, 1908, and the recently described *Taonius notalia* Evans, in prep. *Gonatus phoebetriae* beaks were synonymized with those of *Gonatopsis octopedatus* Sasaki, 1920, thus increasing significantly the number of records and detailing the circumpolar distribution of this rarely caught Southern Ocean squid. The review extends considerably the number of species, including endemics, recorded from the Southern Ocean, but it also highlights that the corresponding species to two well-described beaks (*Moroteuthopsis* sp. B and *Psychroteuthis* sp. B) are still unknown.

Keywords Antarctica · Biogeography · Cephalopods · Predators · Taxonomy · Trophic relationships

Introduction

The cephalopod fauna of the Southern Ocean (Fig. 1) is distinctive. It includes many endemic oceanic squids and benthic octopuses, a single sepiolid, but no cuttlefish (Cherel et al. 2004; Collins and Rodhouse 2006; Rosa et al. 2019). The pelagic squids dominate the oceanic domain, where they occupy the ecological niche shared with epipelagic fish in other oceanic regions (Rodhouse and White 1995; Laptikhovsky et al. 2010). Squids play a major role in the pelagic ecosystem of the Southern Ocean, as underlined by their importance in the diet of predators, which were estimated to consume 12.5–24.0 million tonnes of cephalopods per annum (Santos et al. 2001). This impressive biomass does not translate into an equivalent available body of information on their general biology. Detailed knowledge of Southern Ocean squids is restricted to five subantarctic species that include three non-commercial (*Gonatus antarcticus* Lönnberg, 1898, *Martialia hyadesi* Rochebrune & Mabille, 1889, *Moroteuthopsis ingens* (Smith, 1881)) and two commercially exploited (*Doryteuthis gahi* (d'Orbigny, 1835), *Illex argentinus* (Castellanos, 1960)) species, all being shelf-living organisms at some stages of their life cycle (e.g., Laptikhovsky et al. 2010; Arkhipkin 2013). Much less is known about truly oceanic forms. Our poor understanding of Southern Ocean species, their distribution, and overall biology come from the small number of research cruises targeting squid and octopuses, the difficulties in collecting medium-sized and large cephalopods by nets, together with the paucity of taxonomists and ecologists attracted to the group (Clarke 1996).

Identification of cephalopod prey of fish, seabirds, and marine mammals by using the morphology of their chitinized beaks (Fig. 2) that accumulate in predators'stomach was initiated in the 60s (Clarke 1962a,b). The method was

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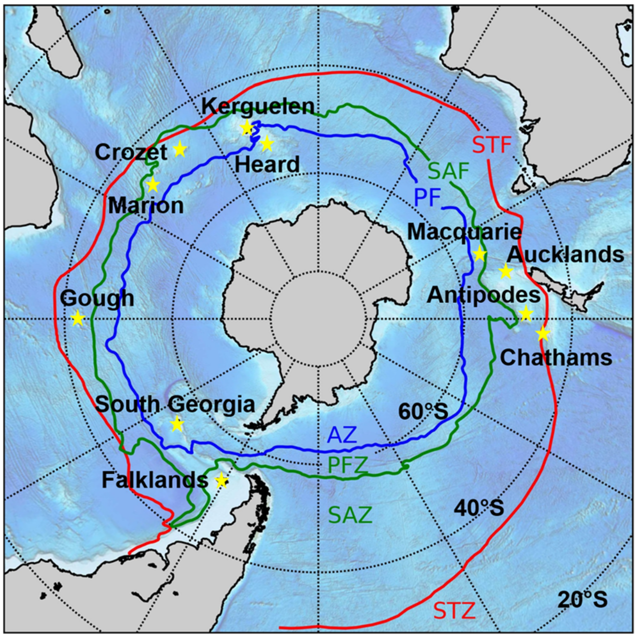

Fig. 1 Map of the Southern Ocean and fringing subtropical waters showing the main islands together with the major oceanic fronts and zones. Abbreviations: AZ, Antarctic Zone; PF, Polar Front; PFZ, Polar Frontal Zone; SAZ, Subantarctic Zone; STF, Subtropical Front; STZ, Subtropical Zone

subsequently developed to investigate the food habits of predators living within the Southern Ocean (see the pioneering work of Imber 1973 and Clarke 1980). A further step was the use of consumers as bio-samplers to describe cephalopod assemblages in ecologically relevant but poorly investigated marine areas (Cherel et al. 2004). Today, more is known about the Southern Ocean cephalopod fauna from dietary studies than from material caught with nets, in spite of the limitations associated with analysis of stomach contents (Rodhouse 2013). Paradoxically, results from dietary investigations were not (or poorly) included in the most recent reviews on

Fig. 2 Wholly darkened lower beaks of three main squid species eaten by wandering albatrosses from the Crozet Islands, from left to right *Moroteuthopsis longimana, Moroteuthopsis ingens*, and *Histioteuthis eltaninae*. Photo and copyright permission from Y Cherel

Southern Ocean cephalopods, thus resulting in an incomplete list of species with an incomplete biogeography (Collins and Rodhouse 2006; Rodhouse 2013; Rodhouse et al. 2014).

Molecular DNA analysis recently boosted significant improvements in squid taxonomy and, accordingly, in the identification of well-known beaks that were still undetermined at the species level (e.g., ?*Mastigoteuthis* A Clarke, 1980, and *Asperoteuthis lui* Salcedo-Vargas, 1999, respectively; Braid 2017). Hence, the time has come to update the Southern Ocean teuthofauna using both net and predator data to synthesize the disparate available information that accumulated over time. The ultimate objective of the review was to facilitate the use of the considerable body of literature to researchers developing programs on this key group of pelagic organisms, their trophic relationships, and overall general biology. Since there was a bias in earlier studies toward Antarctic squids taken with nets in the southwestern Atlantic, a special emphasis was made here on the three previously under-reviewed following topics: (i) the subantarctic teuthofauna and its biogeographic relationships with the Antarctic and subtropical species, (ii) the use of squid-predators as bio-sampling organisms to collect useful information on their prey (Table 1), and (iii) the squid records from the Indian Ocean, which is the less well known of the three major oceans for oceanic pelagic cephalopods.

Material and methods

Physical oceanography and biogeography

The Southern Ocean is here defined as water masses located south of the Subtropical Front (STF). This functional oceanographic definition takes into account all the different branches of the Antarctic Circumpolar Current, with the northernmost branch being the Subantarctic Front (SAF) (Pollard et al. 2002). From North to South, the main marine fronts in that vast oceanic area are the SAF and the Polar Front (PF); they delineate the following oceanic zones within the Southern Ocean, from North to South: the subantarctic Zone (SAZ), Polar Frontal Zone (PFZ), and Antarctic Zone (AZ) (Pollard et al. 2002). The oceanic zone fringing the north of the Southern Ocean is the Subtropical Zone (STZ) (Fig. 1).

According to their distribution, squids were considered as (i) Southern Ocean species if they were recorded from both Antarctic (AZ) and subantarctic (notalian) waters that include the SAZ and PFZ, (ii) Antarctic species if they occur within the AZ (south of the PF) only, and (iii) subantarctic species if they were found between the PF and the STF, meaning within the PFZ (southern subantarctic) and/or the SAZ (northern subantarctic). No new distribution maps were included in the review because the main Southern Ocean squid species were already mapped in detail in previous publications focusing on

Table 1 List of predators of cephalopods that are cited within the review

Family	Common name	Scientific name
Mammals		
Delphinidae	Commerson's dolphin	*Cephalorhynchus commersonii* Lacépède, 1804
	Long-finned pilot whale	*Globicephala melas edwardii* (Traill, 1809)
	Risso's dolphin	*Grampus griseus* (Cuvier, 1812)
Physeteridae	Sperm whale	*Physeter macrocephalus* Linnaeus, 1758
Ziphiidae	Southern bottlenose whale	*Hyperoodon planifrons* (Flower, 1882)
Phocidae	Southern elephant seal	*Mirounga leonina* (Linnaeus, 1758)
	Weddell seal	*Leptonychotes weddellii* (Lesson, 1826)
Otariidae	Antarctic fur seal	*Arctocephalus gazella* Peters, 1875
Birds		
Spheniscidae	Emperor penguin	*Aptenodytes forsteri* Gray, 1844
	King penguin	*Aptenodytes patagonicus* Miller, 1778
	Adélie penguin	*Pygoscelis adeliae* (Hombron & Jacquinot, 1841)
	Northern rockhopper penguin	*Eudyptes moseleyi* (Mathews and Iredale, 1921)
Diomedeidae	Antipodean albatross	*Diomedea antipodensis antipodensis* Robertson & Warham, 1992
	Gibson's albatross	*Diomedea antipodensis gibsoni* Robertson & Warham, 1992
	Northern royal albatross	*Diomedea sanfordi* (Murphy, 1917)
	Southern royal albatross	*Diomedea epomophora* (Forster, 1785)
	Tristan albatross	*Diomedea dabbenena* (Mathews, 1929)
	Wandering albatross	*Diomedea exulans* Linnaeus, 1758
	Black-browed albatross	*Thalassarche melanophris* (Temminck, 1828)
	Gray-headed albatross	*Thalassarche chrysostoma* (Forster, 1785)
	Indian yellow-nosed albatross	*Thalassarche carteri* (Rothschild, 1903)
	Sooty albatross	*Phoebetria fusca* (Hilsenberg, 1822)
	Light-mantled sooty albatross	*Phoebetria palpebrata* (Forster, 1785)
Procellariidae	Black petrel	*Procellaria parkinsoni* (Gray, 1862)
	White-chinned petrel	*Procellaria aequinoctialis* Linnaeus, 1758
	Gray-faced petrel	*Pterodroma gouldi* (Hutton, 1869)
Sharks		
Lamnidae	Porbeagle shark	*Lamna nasus* (Bonnaterre, 1788)
Dalatiidae	Southern sleeper shark	*Somniosus antarcticus* Whitley, 1939
Bony fishes		
Ophidiidae	Pink cusk-eel	*Genypterus blacodes* (Bloch & Schneider, 1801)
Nototheniidae	Antarctic toothfish	*Dissostichus mawsoni* Norman, 1937
	Patagonian toothfish	*Dissostichus eleginoides* Smitt, 1898
Scombridae	Slender tuna	*Allothunnus fallai* Serventy, 1948

Southern Ocean cephalopods (Collins and Rodhouse 2006; Rodhouse et al. 2014; Xavier et al. 2016) and on squids worldwide (Jereb and Roper 2010; Okutani 2015) or regionally (Reid 2016).

Nomenclature

The list of the squid species and their scientific names follow the Tree of Life Web Project (Tolweb, September 2019), except for newly described taxa (e.g., Evans 2018, Fernandez-Alvarez 2018, Kelly 2019). A special emphasis was made to track the different names of species and beaks over the last decades to preclude taxonomic confusion and to facilitate ease of use of the scientific literature. Over the last 30 years, I studied beaks of cephalopods living within the Southern Ocean and in fringing southern subtropical waters using two complementary means, first the progressive building up of a reference collection, and second, the examination of other collections including those from the British Antarctic Survey (PG Rodhouse, 1994 and 1999, England), Port Elizabeth

Museum at Bayworld (NTW Klages, 1996; MJ Smale, 2018, South Africa) and from the Department of Conservation (MJ Imber, 1997, New Zealand). A subset of the beaks identified by Imber and Berruti (1981) was critically examined during my second stay at the Port Elizabeth Museum in 2018. When identifications were conducted by a given scientist or team, it was hypothesized that beak names were consistent over studies and time. Tracking beak names was time-consuming, difficult, but fruitful when identifications were consistently made by one or a few experienced scientists as in England, New Zealand, and South Africa. Overall, beak names of all the most trophically important squids were successfully tracked, but it was not possible to update identification of some rare beaks, for example, *Discoteuthis* sp. and *Discoteuthis* sp. C (Berruti and Harcus 1978; Imber and Berruti 1981; Schramm 1986; Cooper and Klages 1995; Imber 1999; James and Stahl 2000; Cooper and Klages 2009). Identifications were not updated in dietary reviews due to the pooling of many investigations conducted by different teams, and thus of different beak names for a given species (Croxall and Lishman 1987; Prince and Morgan 1987; Cooper and Brown 1990; Cooper et al. 1990; Clarke 1996; Cherel and Klages 1998).

Review of the scientific literature on taxonomy and distribution

A first focus was made on general catalogs either on squids worldwide (Nesis 1987; Jereb and Roper 2010; Okutani 2015; Tolweb 2019) or on cephalopods from the Southern Ocean (Collins and Rodhouse 2006; Rodhouse et al. 2014; Reid 2016; Xavier et al. 2018a). Then, all the articles (1972–2020) and recent gray literature (MSc, PhD) devoted to species, species groups, and assemblages were used to complete and update both taxonomy and biogeography (e.g., Evans 2018, Fernandez-Alvarez 2018, Kelly 2019). Importantly, beaks of four newly-described species were detailed in the present review, with the names of the species descriptors being still provisional, namely the cranchiids *Taonius notalia* and *T. expolitus* (Evans 2018), and the octopoteuthids *Octopoteuthis fenestra* and *Taningia fimbria* (Kelly 2019).

Predators as biological samplers of squids

The review includes all the published dietary investigations of Southern Ocean predators over the period 1973–2019, with Imber (1973) being the oldest significant article on that topic. Three groups of predators were used. First, “resident” squid consumers, meaning that they did not range widely at the short time scale corresponding to their stomach contents. Both fresh and accumulated (beaks with no flesh attached) items were thus considered here, using both the scientific literature and my own data on fish and shark diets within the Southern Ocean. Second, tracking studies showed that subantarctic and Antarctic penguins and pinnipeds remain within the Southern Ocean during breeding. Hence, both their fresh and accumulated squid remains were used to depict the Southern Ocean teuthofauna. Third, by contrast, breeding albatrosses and petrels can forage over long distances, being able to cross the northern boundary of the Southern Ocean (the STF) to feed in the subtropics. Since the presence of flesh indicates prey caught in the vicinity of the colonies, only fresh remains of squids were here considered to detail squid distribution from published and unpublished dietary investigations of flying seabirds. Dietary studies on Southern Ocean seabirds that were conducted outside the Southern Ocean were not considered here.

Lower and upper beaks of squids were identified by comparison with material held in my own collection and by reference to the available literature (Clarke 1980, 1986; Xavier and Cherel 2009).

Results

Detailed analysis of the bibliography listed a total of 60 species of squids recorded south of the STF (Table 2). According to their biogeography, they can be grouped as one circumpolar Antarctic, 13 circumpolar Southern Ocean, 20 circumpolar subantarctic, eight regional subantarctic, and 12 occasional subantarctic species. A critical evaluation removed five species from the list, and one species has an unknown taxonomic status.

Within each group, squid species were listed by alphabetical order. Each species is detailed in two successive paragraphs. The first one summarizes the distribution and taxonomy of the species together with its maximum known mantle length. The second paragraph focuses on the species beaks with a detailed and complete review of the existing literature about their successive names. It ends with a few sentences about the importance of the squid species for Southern Ocean predators, and hence, in the Southern Ocean trophic web.

Circumpolar Antarctic species

***Psychroteuthis glacialis* Thiele, 1920** (Fig. 3): An Antarctic meso-bathypelagic endemic that rarely extends north of the PF; the predominant squid in high-Antarctic waters (Filippova 1972 Fig. 6; Lubimova 1985; Gröger et al. 2000; Xavier et al. 2016). Mantle length to 44 cm (Nesis 1987).

Psychroteuthis glacialis was originally described from incomplete specimens taken from the water surface and from the stomachs of penguins and Weddell seals *Leptonychotes weddellii* (Lesson, 1826) (Thiele 1920). Beaks of the species were well illustrated (Clarke 1986; Xavier and Cherel 2009). They were previously named ?*Psychroteuthis glacialis* (Clarke and MacLeod 1982a, 1982b), *Psychroteuthis* (Clarke 1980), and *Psychroteuthis* sp. (Imber 1991; Croxall

Table 2 List of squid species and their status within the Southern Ocean

Family (alphabetical order)	Species (alphabetical order)	Current status within the Southern Ocean	Southern Ocean endemic	Distribution		
				Antarctic (AZ)	Southern subantarctic (PFZ)	Northern subantarctic (SAZ)
Bathyteuthoidea						
Bathyteuthidae	*Bathyteuthis abyssicola*	Circumpolar Southern Ocean	No	Yes	Yes	Yes
Myopsida						
Loliginidae	*Doryteuthis gahi*	South American subantarctic	No	No	No	Yes
Oegopsida						
Ancistrocheiridae	*Ancistrocheirus lesueurii*	Occasional subantarctic	No	No	No	Yes
Architeuthidae	*Architeuthis dux*	Circumpolar subantarctic	No	(yes)	Yes	Yes
Batoteuthidae	*Batoteuthis skolops*	Circumpolar Southern Ocean	Yes	Yes	Yes	(yes)
Brachioteuthidae	*Brachioteuthis linkovskyi*	Circumpolar subantarctic	No	No	Yes	Yes
	Slosarczykovia circumantarctica	Circumpolar Southern Ocean	Yes	Yes	Yes	(yes)
Chiroteuthidae	*Asperoteuthis lui*	Circumpolar Southern Ocean	Yes	Yes	Yes	Yes
	Chiroteuthis joubini	Occasional subantarctic	No	No	No	Yes
	Chiroteuthis mega	Occasional subantarctic	No	No	No	Yes
	Chiroteuthis veranyi	Circumpolar Southern Ocean	No	Yes	Yes	Yes
	Chiroteuthidae genus C, new?	Status unknown	Status unknown	Yes	No	No
Cranchiidae	*Galiteuthis glacialis*	Circumpolar Southern Ocean	Yes	Yes	Yes	(yes)
	Galiteuthis suhmi	Circumpolar subantarctic	No	No	No	Yes
	Liguriella podophtalma	Circumpolar subantarctic	No	No	Yes	Yes
	Megalocranchia maxima	Occasional subantarctic	No	No	Yes	(yes)
	Mesonychoteuthis hamiltoni	Circumpolar Southern Ocean	Yes	Yes	Yes	Yes
	Taonius notalia	Circumpolar subantarctic	Yes	(yes)	Yes	Yes
	Teuthowenia pellucida	Occasional subantarctic	No	No	Yes	Yes
Cycloteuthidae	*Cycloteuthis sirventi*	Occasional subantarctic	No	No	Yes	Yes
Enoploteuthidae	*Abraliopsis gilchristi*	Occasional subantarctic	No	No	Yes	Yes
	Enoploteuthis semilineata	Pacific subantarctic	No	No	No	Yes
Gonatidae	*Gonatopsis octopedatus*	Circumpolar subantarctic	No	No	Yes	Yes
	Gonatus antarcticus	Circumpolar Southern Ocean	No	Yes	Yes	Yes
Histioteuthidae	*Histioteuthis atlantica*	Circumpolar subantarctic	No	No	Yes	Yes
	Histioteuthis bonnellii corpuscula	Doubtful	No	No	No	No
	Histioteuthis corona	Doubtful	No	No	No	No
	Histioteuthis eltaninae	Circumpolar subantarctic	Yes	(yes)	Yes	Yes
	Histioteuthis macrohista	Occasional subantarctic	No	No	No	Yes
	Histioteuthis miranda	Occasional subantarctic	No	No	No	Yes
	Stigmatoteuthis hoylei/S. arcturi	Doubtful	No	No	No	No
Lepidoteuthidae	*Lepidoteuthis grimaldii*	Doubtful	No	No	No	(no)
Lycoteuthidae	*Lycoteuthis lorigera*	Circumpolar subantarctic	No	No	No	Yes
Mastigoteuthidae	*Mastigoteuthis psychrophila*	Circumpolar Southern Ocean	Yes	Yes	Yes	Yes
	Magnoteuthis osheai	Occasional subantarctic	No	No	No	Yes?

Table 2 (continued)

Family (alphabetical order)	Species (alphabetical order)	Current status within the Southern Ocean	Southern Ocean endemic	Distribution		
				Antarctic (AZ)	Southern subantarctic (PFZ)	Northern subantarctic (SAZ)
Neoteuthidae	*Alluroteuthis antarcticus*	Circumpolar Southern Ocean	Yes	Yes	Yes	No
	Nototeuthis dimegacotyle	Circumpolar subantarctic	Yes	No	Yes	Yes
Octopoteuthidae	*Octopoteuthis fenestra*	Western Pacific subantarctic	Yes	No	No	Yes
	Taningia danae	Circumpolar subantarctic?	No	No	Yes?	Yes
	Taningia fimbria	Circumpolar subantarctic	No	No	Yes?	Yes
Ommastrephidae	*Illex argentinus*	Atlantic subantarctic	No	No	Yes	Yes
	Dosidicus gigas	Occasional Pacific subantarctic	No	No	No	Yes
	Ommastrephes cylindraceus	Atlantic subantarctic	No	No	No	Yes
	Martialia hyadesi	Circumpolar subantarctic	Yes	(yes)	Yes	Yes
	Todarodes cf. *angolensis*	Circumpolar subantarctic?	Yes?	No	Yes	Yes
	Todarodes filippovae	Circumpolar subantarctic	No	No	Yes	Yes
	Nototodarus sloanii	New Zealand subantarctic	Yes	No	No	Yes
Onychoteuthidae	*Filippovia knipovitchi*	Circumpolar Southern Ocean	Yes	Yes	Yes	No
	Moroteuthopsis ingens	Circumpolar subantarctic	Yes	(yes)	Yes	Yes
	Moroteuthopsis longimana	Circumpolar Southern Ocean	Yes	Yes	Yes	No
	Moroteuthopsis sp. B (Imber)	Circumpolar subantarctic	Yes	No	Yes	Yes
	Notonykia africanae	Circumpolar subantarctic	No	No	No	Yes
	Notonykia nesisi	New Zealand subantarctic	Yes	No	No	Yes
	Onykia robsoni	Circumpolar subantarctic	No	(yes)	Yes	Yes
	Walvisteuthis rancureli	Occasional subantarctic	No	No	Yes	(yes)
Pholidoteuthidae	*Pholidoteuthis massyae*	Circumpolar subantarctic	No	(yes)	Yes	Yes
Promachoteuthidae	*Promachoteuthis* sp. B	Pacific subantarctic	No	No	Yes	No?
Psychroteuthidae	*Psychroteuthis glacialis*	Circumpolar Antarctic	Yes	Yes	No	No
	Psychroteuthis sp. B (Imber)	Circumpolar Southern Ocean	Yes	Yes	Yes	No?
Pyroteuthidae	*Pyroteuthis margaritifera*	Doubtful	No	No	No	No

Abbreviations: *AZ* Antarctic Zone (south of the Polar Front), *PFZ* Polar Frontal Zone (between the Polar Front and the Subantarctic Front), *SAZ* Subantarctic Zone (between the Subantarctic Front and the Subtropical Front)

and Prince 1980; Thomas 1982), and they were misidentified as *Discoteuthis* sp. and *Discoteuthis* sp. (small) (Rodhouse et al. 1987, 1990; details in Imber 1992). *Psychroteuthis glacialis* is the most abundant pelagic squid eaten by predators in high-Antarctic waters, including fishes (Stevens et al. 2014), seabirds (Offredo et al. 1985; Ainley et al. 1991; Piatkowski and Pütz 1994; Kirkwood and Robertson 1997), and marine mammals (Rodhouse et al. 1992a; Piatkowski et al. 2002; Daneri et al. 2000; Lake et al. 2003). The species is a common prey of some seabirds that breed within the PFZ but forage southward to Antarctic waters (e.g., the light-mantled sooty albatross *Phoebetria palpebrata* (Forster, 1785) from Kerguelen Islands; YC unpublished data). *Psychroteuthis glacialis* was considered as the main squid eaten by a stranded southern bottlenose whale *Hyperoodon planifrons* (Flower, 1882) from Heard Island (Slip et al. 1995), but a subsequent check indicated misidentification; a subsample of lower beaks ($n = 81$) included beaks from *Mastigoteuthis psychrophila* ($n = 76$, 94%) and *Batoteuthis skolops* ($n = 5$, 6%) (YC unpublished data). It is likely that this misidentification also occurred in the diet of southern elephant seals *Mirounga leonina* (Linnaeus, 1758) (Slip 1995). Beaks initially named ?Large *Psychroteuthis* correspond to those from *Discoteuthis discus* (Clarke 1980; details in Clarke and Roeleved 1998).

Fig. 3 Two specimens of *Psychroteuthis glacialis* collected in the Weddell Sea. Photo and copyright permission from U Piatkowski

Fig. 4 Specimen of *Asperoteuthis lui* collected over the Chatham Rise (New Zealand). Photo and copyright permission from D Stevens

Circumpolar Southern Ocean species

***Alluroteuthis antarcticus* Odhner, 1923**: A circumpolar Southern Ocean meso-bathypelagic endemic that occurs north to the SAF (Xavier et al. 2016; this study). *Alluroteuthis antarcticus* is more abundant within the AZ than further north (Filippova and Yukhov 1982; Xavier et al. 2016). It was previously considered as an Antarctic endemic (Lubimova 1985; Reid 2016; Tolweb 2019), but dietary investigations extended its occurrence to the PFZ, indicating that its northern biogeographical boundary is the SAF. For example, *A. antarcticus* was recorded in small numbers in the stomach of sharks and of the Patagonian toothfish *Dissostichus eleginoides* Smitt, 1898, at the subantarctic Crozet and Kerguelen islands (Cherel and Duhamel 2004; Cherel et al. 2004, 2011), and as fresh items in the diet of the king penguin *Aptenodytes patagonicus* Miller, 1778, at Crozet and the Falkland Islands (Cherel et al. 1996, 2002b). *Parateuthis tunicata* Thiele, 1920, is probably a synonym of *A. antarcticus* (Tolweb 2019; but see Nesis 1987). Mantle length to 27 cm (Nesis 1987).

Beaks of *A. antarcticus* were illustrated in Clarke (1980 Text-fig 207, 1986) and Xavier and Cherel (2009). They were named *Alluroteuthis* sp. (Clarke and McLeod 1982a, b; Adams and Klages 1987; Brown and Klages 1987; Adams and Brown 1989; Green and Burton 1993; Hull 1999) and unidentified (Imber and Russ 1975), and they were misidentified as *Sepioteuthis bilineata* (Imber 1973), *Bathothauma lyromma* (Berruti and Harcus 1978; Imber and Berruti 1981), *Galiteuthis glacialis* (Berruti and Harcus 1978; Imber 1978 Fig. 5F; Berruti 1979; Imber and Berruti 1981; Thomas 1982; Hunter 1983; de L Brooke and Klages 1986; Schramm 1986), ?*Crystalloteuthis glacialis* (Clarke 1980; details in Clarke and Roeleveld 1998), *Crystalloteuthis* sp. (Croxall and Prince 1980; Thomas 1982), (?) *Crystalloteuthis* (Clarke et al. 1981; details in Imber 1992), and *Egea inermis* (Rodhouse et al. 1987; Rodhouse 1989, 1990; details in Imber 1992). *Alluroteuthis antarcticus* is one of the main cephalopod prey of emperor penguins *Aptenodytes forsteri* Gray, 1844, in the Weddell Sea (Piatkowski and Pütz 1994) and of southern elephant seals at Heard and Macquarie Islands (Green and Burton 1993).

***Asperoteuthis lui* Salcedo-Vargas, 1999** (Fig. 4): A circumpolar Southern Ocean meso-bathypelagic endemic that occurs occasionally into the STZ (Clarke 1980; Braid 2017). The species is poorly known. *Asperoteuthis nesisi*, ?*Mastigoteuthis* A, and probably Chiroteuthidae new genus C Young and Roper, 2017, are junior synonyms of *A. lui* (Clarke 1980; Arkhipkin and Laptikhovsky 2008; Braid 2017; Tolweb 2019). Nesis (1987) synonymized *A. lui* (as ?*Mastigoteuthis* A) with Chiroteuthidae new genus B Nesis; however, the taxonomic placement of Chiroteuthidae new genus B is unresolved, being either still considered as a new genus in the family Chiroteuthidae (Braid 2017; Tolweb 2019), or a young stage of *A. lui* (Tolweb 2019). The repartition of *A. lui* was erroneously included in maps referring to *Asperoteuthis acanthoderma* (Jereb and Roper 2010; Okutani 2015; Reid 2016). In its revision of the taxonomy of *A. lui*, Braid (2017) listed 12 specimens known to science, most of them being damaged or very incomplete. Two other specimens with a mantle length of 10.9 and 33.0 cm were caught in pelagic trawls in Kerguelen waters in 1998–1999 (YC unpublished data). Fresh and accumulated beaks of *A. lui* were identified in stomach contents of many predators, thus increasing drastically the number of records. For example, abundance of lower beaks in the diet of sperm whales *Physeter macrocephalus* Linnaeus, 1758, indicates that the species is common in Antarctic waters of the southwest Atlantic (Clarke 1980). Mantle length to at least 36 cm (Arkhipkin and Laptikhovsky 2008; Braid 2017).

Asperoteuthis lui was originally described from a single head obtained from the stomach of a pink cusk-eel *Genypterus blacodes* (Bloch and Schneider, 1801) caught in Cook Strait, New Zealand (Salcedo-Vargas 1999). Its beaks were illustrated in Clarke (1980, 1986) and Xavier and Cherel (2009). Since its original description, the lower beak has been consistently named ?*Mastigoteuthis* A (Clarke 1980, 1986; Lea et al. 2002; Cherel et al. 2002c, 2004, 2011; Cherel and Duhamel 2004; Xavier and Cherel 2009; Richoux et al. 2010; Xavier et al. 2014; Connan et al. 2014; Alvito et al. 2015; Guerreiro et al. 2015; Beasley et al. 2019) or *Mastigoteuthis* A (Clarke and Goodall 1994; Xavier et al. 2011), *Mastigoteuthis* sp. A (Prince 1980b; Clarke et al. 1981; Pascoe et al. 1990; Rodhouse et al. 1987; Rodhouse 1990; Ridoux 1994), *Mastigoteuthis* (large), (small) (Rodhouse et al. 1987; Rodhouse 1990), *Chiroteuthis* sp. D (Imber and Russ 1975; Imber 1992, 1999; James and Stahl 2000), and *Chiroteuthis macrosoma* (Berruti and Harcus 1978; Imber and Berruti 1981). *Asperoteuthis lui* was found in small numbers in the diet of many Southern Ocean predators, including albatrosses and sperm whales (e.g., Clarke 1980; Cherel et al. 2017).

***Bathyteuthis abyssicola* Hoyle, 1885** (Fig. 5): A cosmopolitan meso-bathypelagic species that is abundant in the Southern Ocean where it is the dominant small deep-sea squid (Roper 1969; Xavier et al. 2016). The holotype was collected in the PFZ of the Indian Ocean, between Prince Edward and Crozet Islands (Lipinski et al. 2000). Mantle length to 7.5 cm (Nesis 1987).

Beaks of *B. abyssicola* were illustrated in Clarke (1986), Lu and Ickeringill (2002), and Xavier and Cherel (2009). The species was seldom recorded in the diet of air-breathing vertebrates from the Southern Ocean (Steele and Klages 1986; Clarke and Goodall 1994; Ridoux 1994), most likely due to its deep-sea habits and small size (its tiny beaks can be easily overlooked). It is a rare prey item of the Patagonian toothfish at Kerguelen Islands (YC unpublished data).

***Batoteuthis skolops* Young & Roper 1968** (Fig. 6): A circumpolar Southern Ocean meso-bathypelagic endemic that occurs north to the SAF and probably beyond (Young and Roper 1968; Guerra et al. 2012; Reid 2016). *Batoteuthis skolops* is a rarely reported and poorly known squid. Lubimova (1985) noted that the species is not found in the Indian Ocean, but our data indicate it is a common squid there: (i) *B. skolops* is a prey of albatrosses at Marion and Crozet Islands and (ii) two large specimens with a mantle length of 31.7 and 40.4 cm were caught in bottom trawls in Kerguelen waters in 1999 and 2017, respectively (YC unpublished data). Mantle length to at least 48 cm (Laptikhovsky et al. 2019).

Fig. 5 Specimen of *Bathyteuthis abyssicola* collected in the Ross Sea. Photo and copyright permission from D Stevens

Beaks of *B. skolops* were illustrated in Clarke (1986) and Xavier and Cherel (2009). They were identified as *Batoteuthis* sp. (Ridoux 1994; Kirkwood and Robertson 1997), and they were misidentified as *Mastigoteuthis* sp. D (Imber and Russ 1975), *Chiroteuthis* sp. E (Berruti and Harcus 1978; Berruti 1979; Imber and Berruti 1981; Schramm 1986), and *Chiroteuthis* sp. (Clarke et al. 1981; details in Imber 1992). Most of the beaks that were identified as *Chiroteuthis* sp. in Cooper and Klages (1995), and thus probably in de L Brooke and Klages (1986), Schramm (1986), Hunter and Klages (1989), Lipinski and Jackson (1989), Cooper et al. (1992), Hunter and de L Brooke (1992), Cooper and Klages (2009), and Nel et al. (2000, 2001) refer to *B. skolops* (YC unpublished data), thus indicating that the species is an important cephalopod prey of sooty albatrosses *Phoebetria fusca* (Hilsenberg, 1822) and of gray-headed albatrosses *Thalassarche chrysostoma* (Forster, 1785) from Marion Island. It is also a common prey of wandering albatrosses *Diomedea exulans* Linnaeus, 1758, at the nearby Crozet Islands (Cherel et al. 2017), and of black-browed albatrosses *Thalassarche melanophris* (Temminck, 1828) and gray-headed albatrosses from Diego Ramirez Islands (Arata and Xavier 2003; Arata et al. 2004).

***Chiroteuthis veranyi* Férussac, 1835** (Fig. 7): A circumpolar Southern Ocean and subtropical meso-bathypelagic species that also occurs in the north and equatorial Atlantic and in the Mediterranean (Rodhouse and Lu 1998; Jereb and Roper 2010). A recent DNA analysis suggests that *C. veranyi* is a species complex, since it assigned a different status to the morphologically similar specimens from the North Atlantic/Mediterranean (*C. veranyi*) and from New Zealand (*C.* aff. *veranyi*) (Braid et al. 2017). *Chiroteuthis veranyi* was rarely caught in nets within the Southern Ocean (but see Alexeyev 1994a). However, predators' diet indicates that it is the most common *Chiroteuthis* species living south of the STF, with *C. veranyi* occurring both north and south of the PF (Rodhouse and Lu 1998; Xavier et al. 2002b; Cherel et al. 2004). It was previously identified as *Chiroteuthis* sp. (Rodhouse 1990; Rodhouse et al. 1992b; Rodhouse and Piatkowski 1995). Mantle length to 30 cm (Guerra et al. 2011).

Identification of *Chiroteuthis* beaks was notably difficult due to taxonomic confusion within the family and, consequently, many previous names of beaks in old publications are difficult to interpret. However, the lower beak of *C. veranyi* is well described and illustrated (Clarke 1980 Text-fig 149, 1986; Rodhouse and Lu 1998; Xavier and Cherel 2009), thus being the easiest beak of *Chiroteuthis* to identify in stomach contents of Southern Ocean predators. Lower beaks of *C. veranyi* were previously named *Chiroteuthis* ?*veranyi* (Imber 1973, 1976; Clarke and Prince

Fig. 6 Specimen of *Batoteuthis skolops* collected from a Patagonian toothfish stomach in Kerguelen waters. Photo and copyright permission from N Gasco

1981; Rodhouse 1990), *C. picteti* (Berruti and Harcus 1978; Imber and Berruti 1981; Schramm 1986), *Chiroteuthis* sp. (Vovk et al. 1978; Rodhouse et al. 1990, 1992a; Rodhouse and Prince 1993; Croxall et al. 1997; Berrow and Croxall 1999; Arata and Xavier 2003; Xavier et al. 2003a,b,c, 2004, 2006; Xavier and Croxall 2005), *Chiroteuthis* sp. (small) and *Chiroteuthis* sp. (large) (Rodhouse et al. 1987; Rodhouse 1990; Ridoux 1994), *Chiroteuthis* sp. A (Imber 1973, 1976, 1992, 1999; Imber and Russ 1975; Hunter 1983; James and Stahl 2000), and *Chiroteuthis* sp. C (Clarke 1980, 1986; Clarke and MacLeod 1982c; details in Clarke et al. 1993). Beaks named *C. veranyi* in Berruti and Harcus (1978), Imber and Berruti (1981), and Schramm (1986) referred to *C. joubini* (YC unpublished data). *Chiroteuthis veranyi* is a common but minor prey item of several Southern Ocean predators (e.g., Xavier et al. 2002b, 2014; Cherel and Duhamel 2004; Cherel et al. 2017), and it is the main cephalopod eaten by Patagonian toothfish at Kerguelen Islands (Cherel et al. 2004).

***Filippovia knipovitchi* (Filippova, 1972)** (Fig. 8): A circumpolar Southern Ocean epi-meso-bathypelagic endemic that occurs north to the SAF (Lubimova 1985; Nesis 1987; Nemoto et al. 1988; Bolstad 2010). *Filippovia knipovitchi* was previously named *Moroteuthis knipovitchi* and subsequently *Onykia knipovitchi* (Filippova 1972; Bonnaud et al. 1998; Wakabayashi et al. 2007; Jereb and Roper 2010; Bolstad 2010). It was considered as an Antarctic species (Kubodera et al. 1998; Collins and Rodhouse 2006), but *F. knipovitchi* also occurs within the PFZ, as indicated by its presence in pelagic trawls in Kerguelen waters and by its occurrence as fresh items in the diet of predators at the subantarctic Crozet and Kerguelen Islands (Cherel et al. 1996; Cherel & Weimerskirch 1999; Cherel et al. 2004; YC unpublished data). Mantle length to 45 cm (Kubodera et al. 1998).

Beaks of *F. knipovitchi* are well illustrated (Clarke 1980, 1986; Xavier and Cherel 2009). Its beaks (mainly as *M. knipovichi* or *O. knipovitchi*) are common in predators' stomach contents (e.g., Cherel and Klages 1998; Xavier et al. 2014). The species is one of the main prey of Antarctic toothfish *Dissostichus mawsoni* Norman, 1937, and of sperm whales (Filippova 2002), and it is the major cephalopod prey by mass of southern elephant seal from South Georgia and one of its main food items at Heard and Macquarie islands (Rodhouse et al. 1992a; Green and Burton 1993).

***Galiteuthis glacialis* (Chun, 1906)** (Fig. 9): A circumpolar Southern Ocean meso-bathypelagic endemic that occurs north to the SAF and occasionally to the STF (Lubimova 1985; Guerra et al. 2011; Xavier et al. 2016; Evans 2018). One of the most common squids in Antarctic waters (Rodhouse 1990; Filippova and Pakhomov 1994; Jackson et al. 2002, Lin et al. 2020). It was considered as an Antarctic species (Rodhouse and Clarke 1986; Collins and Rodhouse 2006), but *G. glacialis* also occurs within the PFZ, as indicated by its abundance in pelagic trawls in

Fig. 7 Specimen of *Chiroteuthis veranyi* collected from the Scotia Sea. Photo and copyright permission from JC Xavier

Fig. 8 Specimen of *Filippovia knipovitchi* collected in the northwest of King George Island, Antarctic Peninsula. Photo and copyright permission from U Piatkowski

Fig. 9 Two specimens of *Galiteuthis glacialis* collected in the Scotia Sea (left) and the Ross Sea (right). Photos and copyright permissions from JC Xavier (left) and D Stevens (right)

Kerguelen waters and its occurrence in the diet of predators at the subantarctic Marion, Crozet and Kerguelen Islands (Lubimova 1985; Cherel et al. 2004; YC unpublished data). *Galiteuthis aspera*, *Crystalloteuthis glacialis*, and *Teuthowenia antarctica* are junior synonyms of *G. glacialis* (Filippova 1972; McSweeny 1978; Hopkins 1985). Mantle length to 68 cm (Lin et al. 2020).

Beaks of *G. glacialis* are illustrated in Xavier and Cherel (2009). Its lower beaks were previously named *Galiteuthis* sp. (Clarke and MacLeod 1982b; Green and Burton 1993; Hull 1999) and misidentified as *Galiteuthis armata* (Skinner and Klages 1994), *Teuthowenia antarctica* (Berruti and Harcus 1978; Imber 1978 Fig. 6E; Berruti 1979; Imber and Berruti 1981; Thomas 1982; de L Brooke and Klages 1986; Schramm 1986), *Mesonychoteuthis* sp. A (Croxall and Prince 1980; Prince 1980b; Clarke and Prince 1981; Clarke et al. 1981; Thomas 1982), *Gonatus ?fabricii* (Imber 1973; Johnstone 1977), and ?*Berryteuthis anonychus* (Imber and Russ 1975). It is likely that most of the beaks named *Galiteuthis/Teuthowenia* in Green et al. (1998) belong to *G. glacialis*. In some old articles (Berruti and Harcus 1978; Imber 1978 Fig. 5F; Berruti 1979; Imber and Berruti 1981; Thomas 1982; Hunter 1983; de L Brooke and Klages 1986; Schramm 1986), lower beaks named *G. glacialis* refer to those from *A. antarcticus* (see above). *Galiteuthis glacialis* is eaten by many Southern Ocean predators. Wholly darkened beaks of adult squids are numerous in the diet of several albatrosses (e.g., Cherel and Klages 1998; Cherel et al. 2017), which likely prey or scavenge on dying or dead post-spawning individuals at the sea surface (Nesis et al. 1998a).

Fig. 10 Specimen of *Gonatus antarcticus* collected in the Ross Sea. Photo and copyright permission from D Stevens

Gonatus antarcticus **Lönnberg, 1898** (Fig. 10): A primarily circumpolar subantarctic species that extends south to Antarctic waters and north to the subtropics; the species also occurs off western South America north to ~6°S in cold waters of the Humboldt Current (Kubodera and Okutani 1986 Figs. 3 and 4; Rocha 1997; Nesis 1999). *Gonatus antarcticus* is a meso-bathypelagic species often associated with slope waters, being most abundant in the southwest Atlantic (Rodhouse et al. 1992b; Nesis 1999; Arkhipkin and Laptikhovsky 2010). Mantle length to 40 cm, possibly to 50 cm (Nesis 1999; Laptikhovsky et al. 2007).

Gonatus antarcticus beaks are well illustrated (Clarke 1980, 1986; Xavier and Cherel 2009). They were previously named *Gonatus ?antarcticus* (Prince 1980b), *Gonatus* sp. (Croxall and Prince 1980; Thomas 1982; Lipinski and Jackson 1989; Rodhouse 1990; Robertson et al. 1994; Hull 1999), *Gonatus* sp. A (Clarke et al. 1981), and small ones were misidentified as *Teuthowenia* sp. (Croxall et al. 1985, details in Thompson 1994). Fresh and accumulated beaks of *G. antarcticus* were recorded from stomach contents of many Southern Ocean predators. In agreement with its biogeography and abundance, *G. antarcticus* is a major prey of seabirds at the Falkland Islands, where penguins feed on small juveniles (Thompson 1994). By contrast, Patagonian toothfish from the subantarctic Crozet and Kerguelen Islands and from the Antarctic South Georgia prey upon larger squids that include adult specimens (Xavier et al. 2002b; Cherel et al. 2004). *Gonatus antarcticus* is also a common prey of large procellariiform seabirds from various localities (e.g., Imber 1992; Cherel and Klages 1998; Arata and Xavier 2003; Delord et al. 2010), including the subantarctic Marion, Auckland and Antipodes Islands, and New Zealand mainland (Imber and Berruti 1981; Imber 1999; Xavier et al. 2014). It is also one of the main food items of the southern elephant seal at Heard Island (Green and Burton 1993).

Mastigoteuthis psychrophila **Nesis, 1977** (Fig. 11): A circumpolar Southern Ocean meso-bathypelagic endemic that occurs north to the STF and occasionally in the subtropics (Nesis 1977; Braid and Bolstad 2015, 2019; Tolweb 2019). Mantle length to 18 cm (Rodhouse et al. 2014, Lin et al. 2020).

Fig. 11 Specimen of *Mastigoteuthis psychrophila* collected in the Ross Sea. Photo and copyright permission from D Stevens

Mastigoteuthis psychrophila beaks were illustrated in Xavier and Cherel (2009). They were previously named *Mastigoteuthis* sp. C (Berruti and Harcus 1978; Imber and Berruti 1981) and misidentified as *Psychroteuthis glacialis* (Slip 1995; Slip et al. 1995; see above). It is likely that some unidentified Mastigoteuthidae and *Mastigoteuthis* sp. refer to that species. *Mastigoteuthis psychrophila* beaks were identified as minor items in the diet from various Southern Ocean predators. The species occurred in significant numbers in the diet of Patagonian toothfish from Crozet and Kerguelen waters (Cherel et al. 2004) and it was the main prey of a stranded southern bottlenose whale from Heard Island (Slip et al. 1995). This, together with significant catches in the Prydz Bay region (Lu and Williams 1994a, Lin et al. 2020), indicates that *M. psychrophila* is a common squid in the southern Indian Ocean.

Fig. 12 Specimen of colossal squid *Mesonychoteuthis hamiltoni* collected in the Ross Sea (upper panel) and a tentacular club of the species found in a stomach of Patagonian toothfish caught in Kerguelen waters (lower panel). Photos and copyright permissions from KSR Bolstad (upper panel) and N Gasco (lower panel)

***Mesonychoteuthis hamiltoni* Robson, 1925** (Fig. 12): A circumpolar Southern Ocean meso-bathypelagic endemic that occurs north to the STF and occasionally into the STZ (Lubimova 1985; Xavier et al. 2016). The colossal squid was considered as an Antarctic species (Collins and Rodhouse 2006), but measurements of stable isotope ratios showed a large range of δ^{13}C values that indicate growing from Antarctica to the subtropics (Cherel and Hobson 2005). Indeed, while large specimens and early-life stages were mostly recorded within the AZ, juveniles were caught in both Antarctic and subantarctic waters and sometimes in the subtropics (Nesis 1987; Rodhouse and Clarke 1985; Guerrero-Kommritz 2011). The colossal squid is one of the two largest and heaviest squids, with the species constituting the highest squid biomass in Antarctica (Nesis 1987). Mantle length to 250 cm (possibly to 400 cm, Clarke 1986) and body mass to 500 kg (Jereb and Roper 2010; Remeslo et al. 2019).

Mesonychoteuthis hamiltoni was originally described from two incomplete heads obtained from a sperm whale killed near the South Shetlands (Robson 1925; Lipinski et al. 2000). Beaks of *M. hamiltoni* are well illustrated (Imber 1978 Fig. 6F; Clarke 1980, 1986; Xavier and Cherel 2009). They were named *Mesonychoteuthis* sp. (Yano et al. 2007), and those from *Mesonychoteuthis* sp. A refer to *Galiteuthis glacialis* (Croxall and Prince 1980; Prince 1980b; Clarke and Prince 1981; Clarke et al. 1981; Thomas 1982). *Mesonychoteuthis hamiltoni* is the predominant prey of sperm whales in Antarctic waters, their second food item in subantarctic waters and only a minor item in the subtropics up to 35°S (Klumov and Yukhov 1975; Filippova 2002). It is also a main squid prey of southern sleeper sharks *Somniosus antarcticus* Whitley, 1939, at Kerguelen Islands (Cherel and Duhamel 2004). Beaks of juvenile *M. hamiltoni* were found in small numbers in stomachs of both the Antarctic and Patagonian toothfish (Xavier et al. 2002b; Cherel et al. 2004; Remeslo et al. 2015) and in the diet of albatrosses (Imber 1992; Cherel and Klages 1998).

Fig. 13 Specimen of *Moroteuthopsis longimana* collected in Patagonian slope waters. It was initially described as *Kondakovia nigmatullini* (Laptikhovsky et al. 2008). Photo and copyright permission from V Laptikhovsky

***Moroteuthopsis longimana* (Filippova, 1972)** (Fig. 13): A circumpolar Southern Ocean epi-meso-bathypelagic endemic that occurs north to the SAF (Nemoto et al. 1988; Cherel and Weimerskirch 1999; Xavier et al. 2016). The taxonomic change from *Kondakovia longimana* to *M. longimana* is based on recent DNA phylogenetic analysis (Filippova 1972; Bolstad et al. 2018). *Kondakovia nigmatullini* is a junior synonym of *M. longimana* (Laptikhovsky et al. 2008; Bolstad et al. 2018), and it is likely that *Onychoteuthis* sp. from the diet of sperm whales refers to that species (Mikhalev et al. 1981). *Moroteuthopsis longimana* was considered as an Antarctic species (Lubimova 1985; Kubodera et al. 1998; Collins and Rodhouse 2006; Bolstad 2010) but it also occurs within the PFZ, as indicated by its presence in nets in the Falklands and Kerguelen waters and by its occurrence as fresh items in the diet of predators at the subantarctic Marion, Crozet, and Kerguelen islands (Adams and Klages 1987; Hunter and Klages 1989; Cooper et al. 1992; Cherel et al. 1996; Weimerskirch et al. 1997; Cherel and Weimerskirch 1999; Cherel et al. 2000b, 2017; Nel et al. 2000, 2001; Delord et al. 2010; YC unpublished data). Mantle length to 110 cm, possibly 200 cm (Filippova 2002; Lynnes and Rodhouse 2002; Bolstad 2010).

Beaks of *M. longimana* are well illustrated (Clarke 1980, 1986; Xavier and Cherel 2009). Before the species description (Filippova 1972), beaks of *M. longimana* were named *Moroteuthis ingens* (Clarke 1965, 1966) or undescribed *Moroteuthis* (Clarke 1972), thus leading to taxonomic confusion in old publications (details in Clarke 1980). Afterwards, beaks were consistently named *Kondakovia longimana*, including ?*Kondakovia longimana* (Imber and Russ 1975; Johnstone 1977). Beaks from *K. nigmatullini* were examined and were indistinguishable from those of *M. longimana* (YC unpublished data). *Moroteuthopsis longimana* is eaten by many Southern Ocean predators both as juveniles and adults (e.g., Cherel and Weimerskirch 1999). Owing to its large size, it has a key trophic role in the diet of sleeper sharks, Antarctic and Patagonian toothfish, wandering albatrosses, emperor penguins, southern elephant seals, and sperm whales (Clarke 1980; Nemoto et al. 1988; Rodhouse et al. 1992a; Piatkowski and Pütz 1994; Filippova 2002; Xavier et al. 2002b; Cherel and Duhamel 2004; Cherel et al. 2004, 2017). Wholly darkened beaks indicative of adult squids are numerous in stomach contents of several albatrosses (Imber 1992; Cherel and Weimerskirch 1999), which likely prey or scavenge on dying or dead post-spawning individuals floating at the sea surface (Lu and Williams 1994b; Vacchi et al. 1994; Lynnes and Rodhouse 2002).

***Psychroteuthis* sp. B Imber, 1978**: A second species of the genus *Psychroteuthis* was suggested (Nesis 1987), and a small form of beaks was named *Psychroteuthis* sp. B (Berruti and Harcus 1978; Imber and Berruti 1981; Hunter 1983; Imber 1992), *Psychroteuthis* sp. (Prince 1980a), *Psychroteuthis* sp. A (Ridoux 1994), *P. glacialis* (Rodhouse et al. 1998; Cherel et al. 2004, 2011; Field et al. 2007), *P. glacialis* (small) (Richoux et al. 2010), and unidentified teuthoid (Clarke and MacLeod 1982b). However, no other species was described and the status of *Psychroteuthis* sp. B needs further investigations. It is likely that beaks from *Psychroteuthis* sp. B were not distinguished from (and thus pooled with) those of *P. glacialis* in some investigations. Bimodality in size of wholly darkened beaks is a good indicator of the two *Psychroteuthis* forms in a given dietary investigation, with the small and large modes referring to *Psychroteuthis* sp. B and *P. glacialis*, respectively (details in Rodhouse et al. 1990; Imber 1992). No fresh remains of *Psychroteuthis* sp. B were recorded. The presence of its beaks in stomach contents suggests that it has a circumpolar distribution within the AZ and PFZ but probably not further north.

***Slosarczykovia circumantarctica* Lipinski, 2001** (Fig. 14): A circumpolar Southern Ocean epi-mesopelagic endemic that occurs north to the SAF and occasionally beyond (Lubimova 1985; Guerra et al. 2011; Xavier et al. 2016). Description of the species is still preliminary (Lipinski 2001). *Slosarczykovia circumantarctica* is the only brachioteuthid south of the PF and the most common squid in epipelagic Antarctic waters (Filippova 2002). Before its description, *S. circumantarctica* was named *Brachioteuthis* sp. (Filippova 1972, 2002; Filippova and Pakhomov 1994; Lu and Williams 1994a; Anderson and Rodhouse 2002), *Brachioteuthis picta* (Nemoto et al. 1984, 1985, 1988; Kear 1992; Siegel and Piatkowski 1990; Lancraft et al. 1991, 2004), *Brachioteuthis ?picta* (Rodhouse 1989, 1990; Piatkowski et al. 1994; Rodhouse and Piatkowski 1995; Rodhouse et al. 1996), and *Brachioteuthis riisei* (Lubimova 1985; Nesis 1979, 1987). Mantle length to 18 cm (Guerra et al. 2011).

The lower beak of one paratype of *S. circumantarctica* was examined (Cherel et al. 2004). It showed no strong thickened ridge on the lateral walls (Xavier and Cherel 2009; Tolweb 2019), thus contrasting with beaks from species of the genus *Brachioteuthis* (Clarke 1986). Beaks of *S. circumantarctica* were illustrated in Xavier and Cherel (2009). Its lower beaks were previously named *Brachioteuthis*? (Offredo et al. 1985),

Fig. 14 Specimen of *Slosarczykovia circumantarctica* collected in the Ross Sea. Photo and copyright permission from D Stevens

Brachioteuthis sp. (Cherel and Weimerskirch 1999; Kirkman et al. 2000; Piatkowski et al. 2002; van den Hoff 2004), *Brachioteuthis picta* (Clarke and MacLeod 1982a; Croxall et al. 1999; Lescroël et al. 2004), *Brachioteuthis ?picta* (Rodhouse et al. 1990, 1992a Fig. 1, 1998; Reid 1995; Reid and Arnould 1996; Berrow and Croxall 1999; Berrow et al. 2000; Daneri et al. 1999, 2000, 2005; Pilling et al. 2001; Xavier et al. 2002b, 2003a,b; Arata and Xavier 2003; Arata et al. 2004), *Brachioteuthis riisei* (Clarke and Goodall 1994; Hofmeyr et al. 2010), *Brachioteuthis ?riisei* (Cherel et al. 1996, 2002a,b,c; Catard et al. 2000; Lea et al. 2002), and Oegopsid A (Adams and Klages 1987 Fig. 10; Adams and Brown 1989; Klages et al. 1990; Ridoux 1994). They were misidentified as *Chiroteuthis* sp. (Green and Burton 1993; Slip 1995; Slip et al. 1995), *Mastigoteuthis* sp. (Robinson and Hindell 1996; Goldsworthy et al. 2002), ?*Mastigoteuthis* sp. (Slip et al. 1995; YC unpublished data), *Mastigoteuthis*? (Green et al. 1991, 1997; Green and Wong 1992; Green and Burton 1993; Slip 1995; Moore et al. 1998), and *Teuthowenia pellucida* (Cherel and Ridoux 1992). Many Antarctic and subantarctic predators feed on *S. circumantarctica* (e.g., Abreu et al. 2019) but the species was only found in significant numbers in the diet of the onychoteuthid *Moroteuthopsis ingens* (Cherel and Duhamel 2003), the Patagonian toothfish (Cherel et al. 2004), white-chinned petrel *Procellaria aequinoctialis* Linnaeus, 1758 (Delord et al. 2010), Antarctic fur seal *Arctocephalus gazella* Peters, 1875 (Abreu et al. 2019), and southern elephants seal (Rodhouse et al. 1992a; Slip 1995).

Circumpolar subantarctic species

***Architeuthis dux* Steenstrup, 1857** (Fig. 15): A cosmopolitan meso-bathypelagic species that occurs circumglobally in subantarctic waters and occasionally in Antarctica (Nesis et al. 1985; Förch 1998; Tolweb 2019). Many nominal species were described, with *A. sanctipauli* living in the Southern Hemisphere (Nesis et al. 1985; Förch 1998; Jereb and Roper 2010; Tolweb 2019). However, a morphological investigation found no convincing evidence for more than one species (Förch 1998), which was confirmed by DNA analysis (Winkelmann et al. 2013). *Architeuthis dux* was repeatedly named *Architeuthis* sp. (Vovk et al. 1978; Mikhalev et al. 1981; Alexeyev 1994a; Brunetti et al. 1998; Ré et al. 1998) and also *Architeuthis* sp. B (Rocha 1997). The species was not listed as belonging to the Southern Ocean teuthofauna (Collins and Rodhouse 2006; Rodhouse et al. 2014), while net, stranding, and dietary evidences indicate that *A. dux* occurs in subantarctic waters (Vovk et al. 1978; Nesis 1979; Nesis et al. 1985; Alexeyev 1994a; Brunetti et al. 1998; Förch 1998; Ré et al. 1998; Cherel and Duhamel 2004). The giant squid is one of the two largest and heaviest squids. Mantle length to 300 cm, more often 100–200 cm (possibly to 500 cm), and body mass to 500 kg (Nesis 1987; Reid 2016; Paxton 2016).

Fig. 15 Specimen of giant squid *Architeuthis dux* collected over the Chatham Rise (New Zealand). Photo and copyright permission from D Stevens

Beaks of *A. dux* were well illustrated (Clarke 1980, 1986; Ré et al., 1998; Lu and Ickeringill 2002; Xavier and Cherel 2009). They were previously named *Architeuthis* sp. (Gaskin and Cawthorn 1967a,b; Imber and Russ 1975; Clarke 1980, 1986; Clarke and MacLeod, 1982c; Rodhouse et al. 1987; Rodhouse 1990; Imber 1991, 1992, 1999; Imber and Berruti 1981; Cooper and Klages 1995; Clarke and Roper 1998; Ridoux 1994; Lu and Ickeringill 2002; Xavier et al. 2003b; Xavier and Croxall 2007). The typical lower beak of *A. dux* with or without flesh attached was found in stomach contents of sperm whales caught in subantarctic waters and occasionally in Antarctic waters (Vovk et al. 1978; Clarke 1980; Mikhalev et al. 1981). Large beaks occurred in stomach contents of southern sleeper sharks at Kerguelen Islands and smaller juvenile beaks were recorded in the diet of several albatross species at various localities (Imber 1999; Cherel 2003; Cherel et al. 2017).

***Brachioteuthis linkovskyi* Lipinski, 2001**: A probably circumpolar subantarctic and southern subtropical epi-mesopelagic species. Description of this poorly known squid is still preliminary and was performed on a single specimen caught in the subtropics (Lipinski 2001). MR Lipinski verified the identification of one individual from seven specimens (mantle length 11–16 cm) that were caught with bottom and pelagic trawls in the years 1994–1996 in Kerguelen waters (YC unpublished data). Hence, *B. linkovskyi* co-occurs with the other Southern Ocean brachioteuthid *S. circumantarctica* within the PFZ, as also indicated by the presence of the two species in subsequent numbers in the diet of resident predators from the subantarctic Crozet and Kerguelen Islands (Cherel and Duhamel 2003; Cherel et al. 2004). Before its description, *B. linkovskyi* was likely pooled with *Brachioteuthis picta* (Nesis 1979, 1987). Mantle length to at least 16 cm (YC unpublished data).

The lower beak of the holotype of *B. linkovskyi* was examined (Cherel et al. 2004). It showed a strong thickened ridge on the lateral walls, thus contrasting with beaks from

S. circumantarctica that present no ridge (Xavier and Cherel 2009). Beaks of *B. linkovskyi* were illustrated in Xavier and Cherel (2009). Its lower beaks were previously named *Brachioteuthis* "B" (Xavier et al. 2002b; Arata and Xavier 2003; Arata et al. 2004), *Brachioteuthis* sp. B (Xavier et al. 2003b), *Brachioteuthis* sp. "B" (Clarke) (Pilling et al. 2001; Xavier and Croxall 2007), ?*Brachioteuthis* B (Clarke and Goodall 1994), *Brachioteuthis* sp. (Imber 1992, 1999; Green and Burton 1993; Slip 1995; Slip et al. 1995; Cherel et al. 1996; Goldsworthy et al. 2002; Field et al. 2007), and probably *Brachioteuthis picta* (Clarke 1986 Fig. 44C). Several Southern Ocean predators feed on *B. linkovskyi*, but the species was found in significant numbers in the diet of Patagonian toothfish only (Cherel et al. 2004).

***Galiteuthis suhmi* (Hoyle, 1885)**: A circumpolar subantarctic and southern subtropical meso-bathypelagic species that occurs south to the SAF (Nesis 1979, 1987; Alexeyev 1994a). The holotype was collected in the SAZ south of Australia (Lipinski et al. 2000). A poorly known and rarely reported squid (Alexeyev 1994a; Rocha 1997; Laptikhovsky et al. 2017), with still a confused systematic position (Evans 2018). Mantle length to at least 41 cm (Evans 2018).

The lower beak of the largest specimen from Evans (2018) was examined. It closely matches those of *Galiteuthis* sp. 3 (Imber 1992; YC unpublished data). In previous publications, beaks of *G. suhmi* were either likely confused with those of other squid species or named *Galiteuthis armata* (Clarke and MacLeod 1982c), *Galiteuthis* sp. (Beasley et al. 2019), *Galiteuthis* sp. 3 (Imber 1992, 1999; Xavier and Cherel 2009; Xavier et al. 2014; Cherel et al. 2017), *Megalocranchia maxima* (Imber 1978 Fig. 5D; Imber and Berruti 1981), ?*Taonius megalops* (Clarke 1980), *Teuthowenia megalops* (Clarke 1986; Rodhouse 1990; Clarke and Goodall 1994; Ridoux 1994; Clarke and Roper 1998; Alonso et al. 1999; Cooper and Klages 2009), *Teuthowenia* sp. (Rodhouse et al. 1987; Rodhouse 1990), *Teuthowenia/Megalocranchia* (Ridoux 1994), *Gonatus ?fabricii* (Imber 1973; Johnstone 1977), and *Gonatus* sp. D (Imber and Russ 1975). The species is an important food item of sperm whales in South Africa (Clarke 1980) and an uncommon prey of albatrosses and petrels (Imber 1978, 1992, 1999; Xavier et al. 2014; Cherel et al. 2017).

***Gonatopsis octopedatus* Sasaki, 1920** (Fig. 16): A probably circumpolar subantarctic meso-bathypelagic species, whose main known biogeographic distribution is the western North Pacific (Jereb and Roper 2010; this study). Its rarity in subantarctic waters explains why *G. octopedatus* was not previously listed as belonging to the Southern Ocean teuthofauna (Collins and Rodhouse 2006; Rodhouse et al. 2014). A first specimen from the Falkland Islands was identified as being morphologically and genetically identical to the North Pacific *G. octopedatus* (Arkhipkin et al. 2010). Three new specimens were found in stomach contents of Patagonian toothfish caught

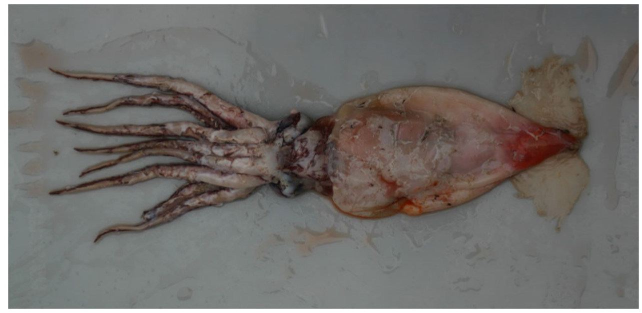

Fig. 16 First specimen of *Gonatopsis octopedatus* caught in the Southern Ocean. It was collected offshore the Falkland Islands (Arkhipkin et al. 2010). Photo and copyright permission from V Laptikhovsky

in Crozet waters. They were badly digested, but four series with two rows of hooks on arms and the absence of tentacles of one head, together with examination of their beaks identified them as *G. octopedatus* (YC unpublished data). Both fresh remains and accumulated beaks from predators' stomachs allowed the quantification of a total of 15 specimens from the southern Atlantic, Indian, and Pacific Oceans (Table 3). Hence, it is likely that they belong to a true Southern Ocean population and were not vagrants from the North Pacific (Arkhipkin et al. 2010). Mantle length to 24 cm (not 39 cm, Jereb and Roper 2010) in the North Pacific (Nesis 1987).

Imber (1978 Fig. 7C) described *Gonatus phoebetriae* based on a single lower beak from the stomach content of a sooty albatross from Marion Island. However, the validity of *G. phoebetriae* was very dubious due to incomplete comparison among beaks in the families and it was considered to be a nomen dubium (Kubodera and Okutani 1986; Nesis 1999; Tolweb 2019). Subsequently, the beaks of *G. phoebetriae* were illustrated, described, and renamed Oegopsida sp. A (Fig. 17) (Cherel et al. 2004). Examination of the lower and upper beaks from the Falkland Island specimen allowed synonymizing Oegopsida sp. A. with *G. octopedatus*. Hence, as expected by MJ Imber, the Southern Ocean teuthofauna does include two gonatid species, but from two distinct genera, *Gonatus* and *Gonatopsis*. Beaks of *G. octopedatus* were previously named *Gonatus phoebetriae* (Berruti and Harcus 1978; Imber 1978 Fig. 7C, 1992; Imber and Berruti 1981; Nesis 1999; Jackson et al. 2007), *Gonatus ?fabricii* (Imber 1973), *Gonatus berryi* (Imber 1978 Fig. 7B; personal communication), and Oegopsida sp. A (Cherel et al. 2004, 2017; Jackson et al. 2007; Xavier and Cherel 2009; Xavier et al. 2014). It is a very rare prey item of Southern Ocean predators (Table 3).

***Histioteuthis atlantica* (Hoyle, 1885)** (Fig. 18): A circumpolar subantarctic and southern subtropical meso-bathypelagic species (Rodhouse et al. 1992b; Voss et al. 1998). A morphological and anatomical examination concluded that *H. atlantica* represents a single species (Voss

Table 3 Records of the gonatid *Gonatopsis octopedatus* in the Southern Hemisphere

Location	Initial identification	Samplers	Sampling Years	Items	Number of Specimens	References
Atlantic Ocean						
South Georgia	*Gonatus phoebetriae*	Wandering albatross	1983–1984	One lower beak	1	Imber (1992)
Falkland Islands	*Gonatopsis octopedatus*	Bottom trawl	2007	One whole specimen	1	Arkhipkin et al. (2010)
Indian Ocean						
Marion Island	*Gonatus phoebetriae*	Sooty albatross	1974–1975	Two lower beaks	2	Imber (1978); Imber and Berruti (1981)
Crozet Islands	Oegopsida sp. A (Cherel)	Patagonian toothfish	1997	One lower and two upper beaks, and one pair	4	Cherel et al. (2004); unpublished data
	Gonatopsis octopedatus	Patagonian toothfish	2010	Three digested specimens	3	This study
Pacific Ocean						
New Zealand	*Gonatus berryi*	Gray-faced petrel	1971	One pair of beaks	1	Imber (1978); personal communication
Auckland Islands	Oegopsida sp. A (Cherel)	Gibson's albatross	2001	One lower beak	1	Xavier et al. (2014)
Antipodes Island	*Gonatus phoebetriae*	Antipodean albatross	1978	One pair of beaks	1	Imber (1992); personal communication
	Gonatus phoebetriae	On the ground (gray petrel?)	1978	One lower beak	1	Imber, personal communication
Total					15	

et al. 1998), but a recent DNA analysis suggests it is a species complex (Braid and Bolstad 2019). *Histioteuthis cookiana* (as in Gaskin and Cawthorn 1967a; Mikhalev et al. 1981) is a junior synonym of *H. atlantica*. While *H. atlantica* is generally outnumbered by *H. eltaninae* in southern subantarctic waters, *H. atlantica* is abundant and the most common histioteuthid at the Kerguelen Islands (Cherel and Duhamel 2004; Cherel et al. 2004). Mantle length to 26 cm (Voss et al. 1998).

Beaks of *H. atlantica* are well illustrated (Clarke 1980 Text-fig 198 and 201, 1986; Lu and Ickeringill 2002; Xavier and Cherel 2009). Distinctive morphological features of the lower beaks separate the histioteuthids in type A and type B beaks (Clarke 1980, 1986). Since *H. atlantica* and *H. eltaninae* belong to the same beak group, the two species were pooled in previous dietary investigations that referred to type B beaks (e.g., Rodhouse et al. 1990, 1992a; Rodhouse and Prince 1993; Ridoux 1994; Arata and Xavier 2003;

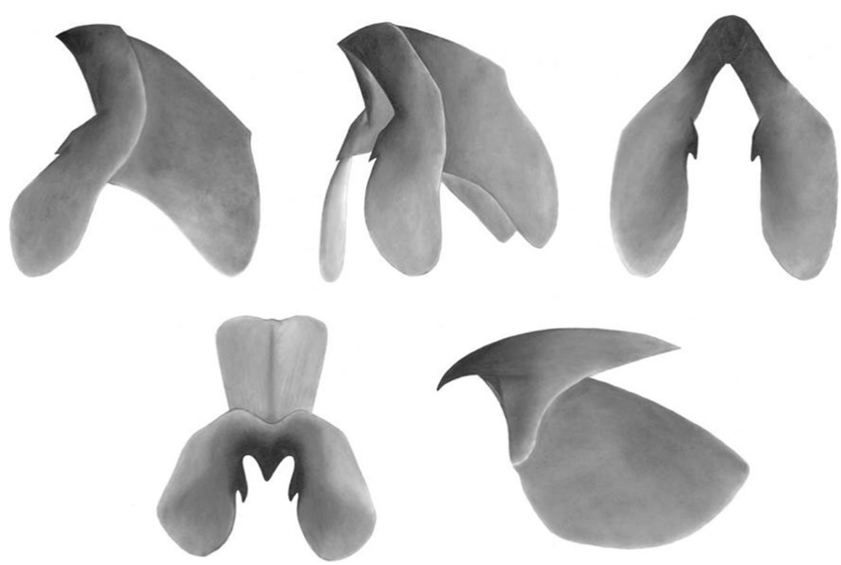

Fig. 17 Drawings of lower and upper beaks of *Gonatopsis octopedatus* (formerly *Gonatus phoebetriae* and Oegopsida sp. A, see text) collected from the stomach content of a Patagonian toothfish caught in Crozet waters (Cherel et al. 2004). Drawings by N Gasco and copyright permission from Marine Ecology Progress Series (Inter-Research Science Publisher)

Fig. 18 Specimen of *Histioteuthis atlantica* collected over the Chatham Rise (New Zealand). Photo and copyright permission from D Stevens

Xavier et al. 2003b; Arata et al. 2004; Xavier and Croxall 2007). However, it is likely that most *Histioteuthis* sp. B in the diet of Southern Ocean predators refer to *H. eltaninae* rather than *H. atlantica* since the former is the most common histioteuthid found in subantarctic waters. *Histioteuthis atlantica* corresponds to beak types B3 and B4 that reach larger sizes than those of *H. eltaninae* (type B1) (Clarke 1980, 1986; Clarke and MacLeod 1982c; Rodhouse et al. 1987; Lipinski 1993). A part of the beaks identified as *H. ?eltaninae* (Imber and Russ 1975; Johnstone 1977) refers to *H. atlantica* (Imber 1992), and beak type C of *Histioteuthis cookiana* also refers to that species (Gaskin and Cawthorn 1967a,b). Several Southern Ocean predators feed on *H. atlantica*, including fish, seabirds, and marine mammals (e.g., Clarke 1980; Clarke and Roper 1998; Imber 1999; Cherel and Duhamel 2004; Cherel et al. 2004). The proportion of *H. atlantica* in the diet of *Diomedea* albatrosses increases and that of *H. eltaninae* decreases with decreasing latitudes, which is in agreement with their respective biogeography (Imber 1992; Cherel et al. 2017).

Histioteuthis eltaninae **Voss, 1969**: A circumpolar subantarctic epi-meso-bathypelagic endemic that occurs occasionally further south into the AZ and further north into the STZ (Voss et al. 1998; Reid 2016; Xavier et al. 2016). *Histioteuthis eltaninae* is the only histioteuthid recorded south of the PF (Collins et al. 2004) and it is the most common histioteuthid found in subantarctic waters, being most abundant in the southern half of the region (Voss 1969; Voss et al. 1998). In contrast to the Atlantic and Pacific Oceans, *H. eltaninae* was rarely reported from the southern Indian Ocean (Voss et al. 1998). However, it was caught in nets in Kerguelen waters over the last decades (YC unpublished data) and the species is a common food item of many predators from Marion, Crozet and Kerguelen islands, thus indicating that it is an abundant squid inhabiting the PFZ of the Indian Ocean. Mantle length to 11 cm (Nesis 1987).

Beaks of *H. eltaninae* are well illustrated (Clarke 1980 Text-fig 195 and 196, 1986; Lu and Ickeringill 2002; Xavier and Cherel 2009). Since morphological features indicate that lower beaks from both *H. eltaninae* and *H. atlantica* belong to type B of histioteuthid beaks, the two species were pooled in dietary investigations that referred to type B beaks (see above). In agreement with their biogeography, a subsequent re-examination of some beaks showed a predominance of *H. eltaninae* over *H. atlantica* in the diet of seabirds from the subantarctic Crozet Islands (Ridoux 1994; YC unpublished data). *Histioteuthis eltaninae* corresponds to beak type B1 (Clarke 1980, 1986), which was also named *H. ?eltaninae* (Clarke 1980; Croxall and Prince 1980; Clarke and Prince 1981; Clarke et al. 1981; Rodhouse 1990). It is likely that *H. reversa* (beak type B2) identified in the diet of sperm whales off South Africa (Clarke 1980) refers to *H. eltaninae* because beaks of the two species are closely related (Clarke 1986; YC unpublished data) and *H. reversa* does not occur in the area (Voss et al. 1998). *Histioteuthis eltaninae* is an abundant prey item and the most common histioteuthid in the diet of Patagonian toothfish and albatrosses from South Georgia, Marion, and Crozet islands (Imber and Berruti 1981; Rodhouse et al. 1987; Hunter and Klages 1989; Cooper et al. 1992; Cherel and Klages 1998; Cherel et al. 2004, 2017). It is the main cephalopod prey of southern elephant seals at Macquarie Island (Green and Burton 1993).

Liguriella podophtalma **Issel, 1908**: A circumpolar subantarctic and bi-subtropical epi-meso-bathypelagic species (Nesis 1987) that also occurs in the tropics (Evans 2018). A poorly known and rarely reported squid (Laptikhovsky et al. 2017; Evans 2018). Mantle length to 24 cm (Jereb and Roper 2010).

The lower beak of a 23-cm mantle length *L. podophtalma* from New Zealand was examined. It matched those of *Galiteuthis* stC sp. by Imber (1992), with StC being an acronym for Subtropical Convergence (STF in the present study). *Galiteuthis* stC sp. was subsequently identified in Imber (1999), Cherel et al. (2004), Xavier and Cherel (2009), Xavier et al. (2014), and Cherel et al. (2017). Beaks of *L. podophtalma* were also named *Taonius belone* (Berruti and Harcus 1978; Imber 1978 Figs. 4 and 5C; Imber and Berruti 1981; Schramm 1986; details in Imber 1992), *Taonius* sp. B (Imber 1973), *Galiteuthis* "*armata*" (Clarke and Goodall 1994), and *Galiteuthis armata*, which included a few smaller beaks that probably referred to *Galiteuthis glacialis* (Clarke 1980, 1986; Clarke and Roper 1998; YC unpublished data). Beaks of *L. podophtalma* were found in the diet of the Patagonian toothfish at Crozet Islands (Cherel et al. 2004), albatrosses from various localities, sperm whales from South Africa and Australia, and southern bottlenosed whales from Tierra del Fuego (Clarke 1980; Imber 1992,

Fig. 19 Specimen of *Lycoteuthis lorigera* collected in New Zealand subantarctic waters. Photo and copyright permission from D Stevens

1999; Clarke and Goodall 1994; Xavier et al. 2014; Cherel et al. 2017).

***Lycoteuthis lorigera* (Steenstrup, 1875)** (Fig. 19): A circumpolar subantarctic and southern subtropical nerito-oceanic meso-bathypelagic species that occurs south to the SAF (Nesis 1987; Villanueva and Sanchez 1993; Alexeyev 1994a). While it is sometimes assumed that *L. lorigera* is also an Antarctic species (Filippova 1972), it does not occur within the AZ. *Lycoteuthis diadema* and *Oregoniateuthis lorigera* are junior synonyms of *L. lorigera* (Villanueva and Sanchez 1993). Mantle length to 19 cm (Förch and Uozumi 1990).

Lycoteuthis lorigera was originally described from two specimens found in the stomach content of sperm whales (details in Villanueva and Sanchez 1993). Beaks of *L. lorigera* are illustrated in Lu and Ickeringill (2002) and Xavier and Cherel (2009). Its lower beak was previously named *Lycoteuthis* sp., *Lycoteuthis* sp. A and *Lycoteuthis* sp. B (Rodhouse 1990; Ridoux 1994), *L. diadema*, *L. longimanus*, *Oregoniateuthis longimanus* (Imber 1975, 1976, 1999; Clarke 1986), and *Oregoniateuthis* sp. (Thomas 1982). *Lycoteuthis lorigera* occurs rarely in the diet of Southern Ocean predators (e.g., Imber 1999; Cherel et al. 2017). However, it is the most common cephalopod prey of the black petrel *Procellaria parkinsoni* (Gray, 1862), which breeds further north in the subtropics (Imber 1975).

***Martialia hyadesi* Rochebrune & Mabille, 1889**: A circumpolar subantarctic oceanic-neritic epi-mesopelagic endemic that occurs occasionally into the AZ (Rodhouse and Yeatman 1990; Alexeyev 1994a; Wormuth 1998; Xavier et al. 2016). The distribution of *M. hyadesi* is related to the PFZ in the southwest Atlantic (Rodhouse 1991), and to the STF near New Zealand (Uozumi et al. 1991). A few specimens of *M. hyadesi* were caught in the Indian Ocean (Piatkowski et al. 1991; Rodhouse 1997; YC unpublished data), but its abundance in the diet of predators indicate the species commonly occurs in Marion, Crozet, and Kerguelen waters (Cherel et al. 1996, 2000b, 2002c, 2004, 2011, 2017; Weimerskirch et al. 1997; Nel et al. 2000, 2001). Protein analysis showed genetic differentiation across the *M. hyadesi* range, suggesting cryptic speciation amongst morphologically similar specimens (Brierley et al. 1993). Mantle length to 51 cm (Rodhouse et al. 1996).

Beaks of *M. hyadesi* were illustrated in Rodhouse and Yeatman (1990), and Xavier and Cherel (2009). Its lower beaks were previously named *Todarodes sagittatus* (Croxall and Prince 1980; Prince 1980b; Thomas 1982), *Todarodes ?sagittatus* (Clarke and Prince 1981; Clarke et al. 1981; Kock 1987; details in Rodhouse 1990), and *Martialia* (Green and Burton 1993). It is likely that beaks of *M. hyadesi* were confused and pooled with those of *Todarodes filippovae* in the diet of seabirds from the Crozet Islands (Ridoux 1994). *Martialia hyadesi* is a common prey of Southern Ocean predators (e.g., Rodhouse et al. 1993). Juveniles constitute the main cephalopod eaten by the king penguin, *Thalassarche* albatrosses, white-chinned petrel, and by the slender tuna *Allothunnus fallai* Serventy, 1948 (Prince 1980b; Croxall et al. 1995; Yatsu 1995; Cherel and Klages 1998; Rodhouse et al. 1998; Waugh et al. 1999), while larger specimens are caught by *Diomedea* albatrosses, the southern elephant seal and Patagonian toothfish (Rodhouse et al. 1992a; Cherel et al. 2004, 2017).

***Moroteuthopsis ingens* (Smith, 1881)** (Fig. 20): A circumpolar subantarctic oceanic-neritic epi-meso-bathypelagic endemic that occurs occasionally into the AZ (Lubimova 1985; Jackson et al. 2000b; Xavier et al. 2016). *Moroteuthopsis ingens* is abundant at the bottom of slopes surrounding subantarctic islands, namely the Falklands, Crozet, Kerguelen, and Macquarie islands, and in subantarctic waters of southern Tasmania and New Zealand. *Moroteuthopsis ingens* was previously named *Moroteuthis* sp. and Onychoteuthidae (Gaskin and Cawthorn 1967a,b), *Moroteuthis ingens*, and subsequently *Onykia ingens* (Bolstad 2010). The taxonomic change from *O. ingens* to *Moroteuthopsis ingens* is based on a recent DNA phylogenetic investigation (Bolstad et al. 2018). DNA analyses showed high levels of variation between individuals (Sands et al. 2003) and suggest *M. ingens* includes more than one species (Bolstad et al. 2018). Mantle length to 58 cm (Jackson and Jackson 2004).

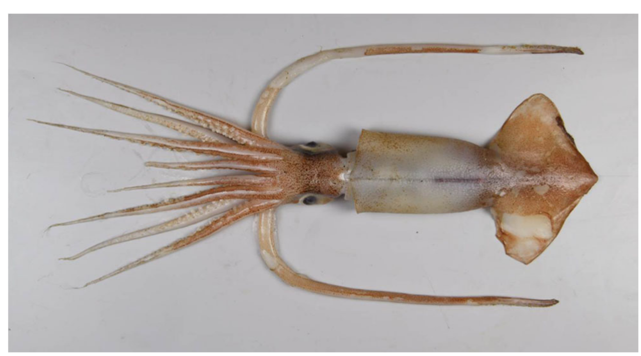

Fig. 20 Specimen of *Moroteuthopsis ingens* collected in New Zealand subantarctic waters. Photo and copyright permission from D Stevens

Beaks of *M. ingens* are well illustrated (Clarke 1980 Text-fig 90, 1986; Lu and Ickeringill 2002; Bolstad 2006; Xavier and Cherel 2009). Its lower beaks were previously named types Aii (= *Moroteuthis* sp.) and Aiii (= Onychoteuthidae) beaks (Gaskin and Cawthorn 1967a,b; details in Clarke and Roper 1998), and *Moroteuthis* A (Clarke 1980; Clarke and MacLeod 1982c; details in Clarke 1986 and Clarke and Roeleveld 1998). Some confusion occurred between beaks from *M. ingens* and those from *M. longimana* before description of the latter species (see *M. longimana* above). Lower beaks from large juveniles and adults of *M. ingens* showed sexual dimorphism in size and morphology that allows differentiating males and females (Bolstad 2006; Xavier and Cherel 2009). Beaks from *M. ingens* (as *Moroteuthis ingens* or *O. ingens*) are common items in predators' stomach contents (e.g., Jackson et al. 1998; Cherel and Weimerskirch 1999). Small- and medium-sized juveniles are eaten by fish (Yatsu 1995; Jackson et al. 2000a; Cherel et al. 2004) and penguins (Cherel et al. 1996; Moore et al. 1998), while adults are targeted by albatrosses (Imber 1992, 1999; Cherel et al. 2017) and marine mammals (Gaskin and Cawthorn 1967b; Green and Burton 1993; Clarke and Goodall 1994). Albatrosses probably prey or scavenge on post-spawning dying or dead individuals that show tissue degeneration (Jackson and Mladenov 1994) and likely positive buoyancy (Laptikhovsky et al. 2007).

***Moroteuthopsis* sp. B Imber, 1992**: A likely circumpolar subantarctic epi-mesopelagic endemic. Imber (1992, Fig. 1a) described unknown onychoteuthid beaks as *Moroteuthopsis* sp. B because they share features with those of *M. ingens*. They were illustrated in Cherel et al. (2004) (Fig. 21) and Xavier and Cherel (2009). While fresh remains of *Moroteuthopsis* sp. B in predators' diet are rare, the tentacular club morphology of one badly digested specimen confirmed that the species is an onychoteuthid, showing a well-defined carpus and a manus with both suckers and (scars of) hooks (YC unpublished data). Beaks of *Moroteuthopsis* sp. B are notably different from those of all other onychoteuthids known to live within the Southern Ocean, thus indicating that it corresponds to a still undescribed species. The size of adult *Moroteuthopsis* sp. B is unknown, but its largest lower beaks are smaller than those of *M. longimana*, *Onykia robsoni*, and *F. knipovitchi* and they are larger than those of *Notonykia africanae* (Cherel et al. 2004, 2017), thus suggesting it is a medium-sized onychoteuthid.

Lower beaks of *Moroteuthopsis* sp. B were likely confused with those from other onychoteuthids. For example, they were pooled with beaks of *Filippovia knipovitchi* in the diet of southern elephant seals from Macquarie Island (Field et al. 2007; YC unpublished data). The lower beak of *Moroteuthopsis* sp. B was named "undescribed gen. & sp." (Berruti and Harcus 1978; Imber and Berruti 1981) and *Onychoteuthis* sp. (ridge) (Ridoux 1994) before its description, and *Moroteuthis* sp. B thereafter (Cherel and Weimerskirch 1999; Cherel et al. 2000b, 2002b,c, 2004; Wienecke and Robertson 2006; Xavier and Cherel 2009; Delord et al. 2010; Xavier et al. 2014; Alvito et al. 2015; Velez-Rubio et al. 2015). *Moroteuthopsis* sp. B is not a main prey of any predator, but its beaks were regularly identified in stomach contents of fish, penguins, albatrosses, and petrels at various localities from the Atlantic, Indian, and Pacific Oceans (Imber and Berruti 1981; Imber 1992, 1999; Cherel and Weimerskirch 1999; Cherel et al. 2000b, 2002b,c, 2004, 2017; Delord et al. 2010; Xavier et al. 2014, 2018b, Alvito et al. 2015; Velez-Rubio et al. 2015). Altogether, information from predators indicates that the species has a circumpolar distribution in subantarctic waters, with occasional records within the STZ but not south of the PF. Since it is a food item of the deep-diving king penguin that feeds on live prey in oceanic waters (Cherel and Weimerskirch 1999; Cherel et al. 2002b), *Moroteuthopsis* sp. B occurs at least in the epi- and mesopelagic layers of the water column.

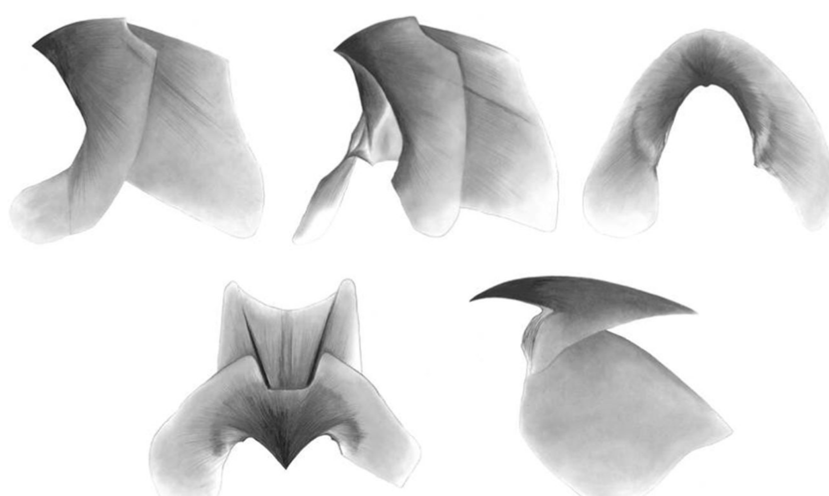

Fig. 21 Drawings of lower and upper beaks of *Moroteuthis* sp. B. collected from the stomach content of a Patagonian toothfish caught in Kerguelen waters (Cherel et al. 2004). Drawings by N Gasco and copyright permission from Marine Ecology Progress Series (Inter-Research Science Publisher)

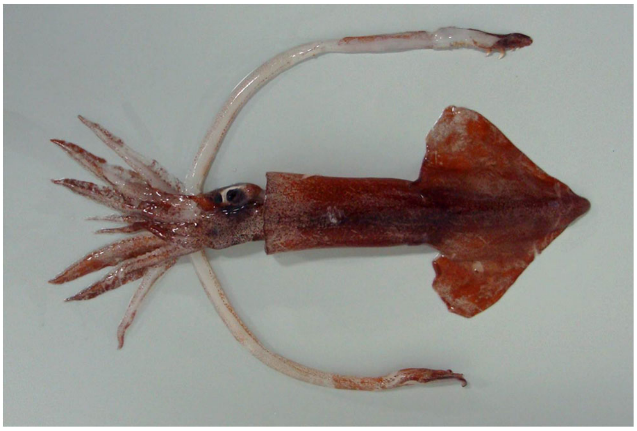

Fig. 22 Specimen of *Notonykia africanae* collected over the Chatham Rise (New Zealand). Photo and copyright permission from D Stevens

***Notonykia africanae* Nesis, Roeleveld & Nikitina, 1998** (Fig. 22): A circumpolar subantarctic and southern subtropical epi-meso-bathypelagic species that occurs south to the SAF (Nesis et al. 1998b; Bolstad 2007, 2010). *Notonykia africanae* was previously reported as *Onykia* (?) *verrilli,* "*Onykia*" *verrilli*, *Ancistroteuthis lichtensteinii* South Atlantic form, and Onychoteuthidae, new genus and species, in publications relevant to the Southern Ocean teuthofauna (Nesis 1979, 1987; Alexeyev 1994a; Rocha 1997; Kubodera et al. 1998; Roeleveld 1998; see also Nesis et al. 1998b). Maximum known mantle length to 20 cm (Bolstad 2007, 2010).

Beaks of *N. africanae* were illustrated and photographed (Nesis et al. 1998b; Bolstad 2010; Tolweb 2019). The lower beak was first poorly described as *Onychoteuthis* sp. B (Imber 1992) before examination of beaks from two paratypes synonymized *Onychoteuthis* sp. B with *N. africanae* (YC unpublished data). Paratype beaks were smaller than those found in predators' stomach contents, thus indicating that mature individuals reach a larger size than the examined specimens (54 and 118 mm ML). Beaks from *N. africanae* were previously identified as *Onychoteuthis banksi* (Imber and Russ 1975, details in Imber 1992), *Onychoteuthis* sp. B (Imber 1992, 1999; James and Stahl 2000), and *Onychoteuthis* sp. (large) (Ridoux 1994). The species is a rare prey item of Southern Ocean albatrosses (Imber 1992, 1999; Xavier et al. 2014; Cherel et al. 2017).

***Nototeuthis dimegacotyle* Nesis & Nikitina, 1986**: A circumpolar subantarctic meso-bathypelagic endemic (Nesis and Nikitina 1992; Jereb and Roper 2010). *Nototeuthis dimegacotyle* is recorded from a few small- to medium-sized specimens (Tolweb 2019), but it was reported as being rather common in subantarctic waters of the Pacific Ocean (Alexeyev 1994a). New records together with flesh remains and beaks from predators' stomach contents indicate that *N. dimegacotyle* also occurs in the southern Indian (Crozet, Kerguelen) and Atlantic Oceans, and possibly in subtropical waters (Amsterdam Island) (Anderson and Rodhouse 2002; Cherel et al. 2004; YC unpublished data). The species was initially named "n. gen. & sp. Nesis & Nikitina" (Nesis 1987) and subsequently described as *N. dimegacotyle* (Nesis and Nikitina 1986). The largest specimen reported in the literature is an immature female 8.3 cm ML (Nesis and Nikitina 1992). However, a ~ 24 cm-ML damaged male was found in the stomach of a Patagonian toothfish caught in Kerguelen waters, and lower rostral length of accumulated beaks indicate *N. dimegacotyle* can reach a larger size (YC unpublished data).

Beaks of *N. dimegacotyle* were initially described and illustrated from nine specimens collected as prey of the Patagonian toothfish at Crozet and Kerguelen Islands in 1995 (Cherel et al. 2004; Xavier and Cherel 2009; YC unpublished data). Its lower beaks were likely confused and/or pooled with beaks from other squid species in publications older than the date of its description. For example, *N. dimegacotyle* was previously misidentified as Cranchiidae sp. E and *Sepioteuthis bilineata* (Imber 1973), *Cranchia scabra* (Imber 1978 Fig. 2, 1992), *Galiteuthis* sp. A (Imber 1976), *Galiteuthis armata* (Berruti and Harcus 1978; Imber 1978 Fig. 5E; Imber and Berruti 1981; Schramm 1986), *Helicocranchia* sp. (Rodhouse et al. 1987; Rodhouse 1990), and it was subsequently named ?*N. dimegacotyle* (Imber 1999; James and Stahl 2000). Fully darkened beaks of *N. dimegacotyle* were found in stomach contents of fish, seabirds, and marine mammals, being significant in the diet of the Patagonian toothfish from Kerguelen Islands only (Cherel et al. 2000b, 2004, 2017; Xavier et al. 2014, Alvito et al. 2015; Beasley et al. 2019).

***Onykia robsoni* (Adam, 1962)** (Fig. 23): A circumpolar subantarctic and southern subtropical meso-bathypelagic species that was recorded occasionally south of the PF (South Georgia); *O. robsoni* possibly occurs in the North Atlantic (Clarke 1980; Nesis 1987; Kubodera et al. 1998; Bolstad 2010; Rodhouse et al. 2014; Reid 2016). However, a recent molecular phylogeny revealed that morphologically similar *O. robsoni* include four genetically distinct taxa, i.e., one North Atlantic and three Southern Ocean species (Bolstad et al. 2018). *Onykia robsoni* was previously named

Fig. 23 Specimen of *Onykia robsoni* collected in New Zealand subantarctic waters. Photo and copyright permission from D Stevens

Moroteuthis robsoni until *Moroteuthis* was considered a junior synonym of *Onykia* (Tsuchiya and Okutani 1991; Bolstad 2010). Four large specimens (51–68 cm ML) were by-caught in benthic trawls in Kerguelen waters in 1999. Mantle length to 75 cm (Nesis 1987).

Beaks of *O. robsoni* are well illustrated (Clarke 1980, 1986; Lu and Ickeringill 2002; Xavier and Cherel 2009). Its lower beaks (mainly as *M. robsoni*) were regularly identified from Southern Ocean predators' stomach contents, including fish, sharks, seabirds, and marine mammals (e.g., Cherel and Duhamel 2004; Cherel et al. 2004, 2017; Xavier et al. 2014; Cherel et al. 2017). It is a significant prey item of sperm whales south and north of the STF (Vovk et al. 1978; Clarke and MacLeod, 1982c).

Pholidoteuthis massyae **(Pfeffer, 1912)** (Fig. 24): A circumpolar subantarctic and southern subtropical meso-bathypelagic species that was recorded occasionally south of the PF (Nemoto et al. 1988; Alexeyev 1994a; Jackson et al. 2002; Jereb and Roper 2010). *Pholidoteuthis massyae* was previously named *Pholidoteuthis boschmai* (Clarke 1980; Nemoto et al. 1984, 1985, 1988; Alexeyev 1994a; Jackson et al. 2002; Collins and Rodhouse 2006), and *Pholidoteuthis* sp. and *Tetronychoteuthis dussumieri* (Vovk et al. 1978). Two revisions clarified this confused taxonomy by invalidating the genus *Tetronychoteuthis* and by classifying *P. boschmai* and *T. dussumieri* as conspecific with *P. massyae* (Nesis and Nikitina 1990; O'Shea et al. 2007). Mantle length to 72 cm (Jereb and Roper 2010).

Beaks of *P. massyae* are well illustrated (Clarke 1980, 1986; Lu and Ickeringill 2002; Xavier and Cherel 2009). Its distinctive lower beaks were previously named beak type Bi (Gaskin and Cawthorn 1967a,b), *Pholidoteuthis*? (Offredo et al. 1985), *Pholidoteuthis* sp. (Green and Burton 1993; Ridoux 1994; Cooper and Klages 1995; Hull 1999), *P. boschmai* (Clarke 1980, 1986; Clarke et al. 1981; Rodhouse et al. 1987; Lipinski and Jackson 1989; Rodhouse 1990; Cooper et al. 1992; Imber 1992, 1999; van den Hoff 2001, 2004; Lu and Ickeringill 2002; Xavier et al. 2003b; Xavier and Croxall 2007; Cherel et al. 2002c, 2004, 2011; Field et al. 2007), *P. boschmai* A and B (Clarke and MacLeod, 1982c), and ?*Tetronychoteuthis* sp. (Imber 1992). According to size and morphology, beaks of *P. massyae* eaten by sperm whales clustered into three groups, thus suggesting that there may well be three species in the Southern Hemisphere (Clarke 1986). Beaks of *P. massyae* possibly show sexual dimorphism (O'Shea et al. 2007), but examination of additional specimens is needed to test if beak morphology allows differentiating males and females. Within the Southern Ocean, *P. massyae* is a prey of fish, seabirds, and marine mammals, but usually in low numbers (e.g., Clarke 1980; Clarke and MacLeod, 1982c; Ridoux 1994; Cherel et al. 2004, 2017).

Taningia danae **Joubin, 1931**, and ***Taningia fimbria*** **Kelly, in prep** (as cited in Kelly 2019) (Fig. 25): A recent taxonomic revision split the monotypic *T. danae* sensu *lato* (*s.l.*) into five different taxa, including two species that were collected within the Southern Ocean, namely *T. danae* sensu stricto (*s.s.*) and the newly described *T. fimbria* (Kelly 2019). Since most previously identified specimens and beaks cannot be reliably identified as *T. danae s.s.* or *T. fimbria*, I first synthesized the available information on *T. danae s.l.* and then added a few words about the new taxonomy.

Taningia danae s.l. was considered as a cosmopolitan meso-bathypelagic species that occurs south to the PF (Nesis 1987; Roper and Vecchione 1993; Jereb and Roper 2010). It was not previously listed within the Southern Ocean teuthofauna (Collins and Rodhouse 2006; Rodhouse et al. 2014), while both predators' diet and net catches indicate the species occurs in subantarctic waters but is absent from the Antarctic (Clarke 1967, 1980). For example, it was recorded in Kerguelen Islands by both its presence in fish diet (Cherel and Duhamel 2004; Cherel et al. 2004) and the catch of two specimens in bottom trawls (~ 60 and 29 cm ML in 1994 and 1995, respectively; YC unpublished data). *Taningia danae s.l.* was identified as *Cucioteuthis* sp. in the diet of sperm whales (Mikhalev et al. 1981). Mantle length to 170 cm (Nesis 1987).

Fig. 24 Specimen of *Pholidoteuthis massyae* collected in New Zealand waters. Photo and copyright permission from D Stevens

Fig. 25 Specimen of *Taningia fimbria* collected over the Chatham Rise (New Zealand). Photo and copyright permission from D Stevens

Beaks of *T. danae s.l.* are well illustrated (Clarke 1980, 1986; Lu and Ickeringill 2002; Xavier and Cherel 2009). They were previously named *Taningia* sp. (Ridoux 1994) and ?*T. danae* (Imber and Russ 1975). Beaks were recorded from stomach contents of many Southern Ocean predators, including fish, seabirds, and marine mammals (e.g., Imber 1992, 1999; Cherel et al. 2004, 2017), with the species being a significant prey item of southern sleeper sharks and sperm whales (Clarke 1980; Clarke and MacLeod 1982c; Cherel and Duhamel 2004). The size of lower beaks from *T. danae s.l.* eaten by sperm whales in the Tasman Sea suggests that two species are involved, one not yet described (Clarke and MacLeod 1982c; Clarke 1986).

In his taxonomic revision, Kelly (2019) examined 75 specimens of *T. danae s.s.* (mantle length to > 131 cm, possibly to 160 cm) and 35 specimens of *T. fimbria* (mantle length to 97 cm). *Taningia danae s.s.* is a cosmopolitan species. In the Southern Hemisphere, it occurs primarily in tropical and subtropical waters and occasionnaly within the SAZ. In contrast, *T. fimbria* was recorded only in the Southern Hemisphere, where it is circumpolar in the STZ and SAZ. *Taningia fimbria* outnumbers *T. danae s.s.* in the Southern Ocean, being the most southerly distributed octopoteuthid (Kelly 2019). However, it has not yet been recorded further south, into the PFZ, where *T. danae s.l.* is known to occur (see above). Hence, the specific status of the southernmost specimens of *Taningia* remains to be determined. Beaks of the two species are well illustrated and look pretty similar (Kelly 2019). No dietary studies yet refer to the recently described *T. fimbria*.

***Taonius notalia* Evans, in prep** (as cited in Evans 2018): A circumpolar subantarctic meso-bathypelagic endemic that occurs occasionally south of the PF (Evans 2018). *Taonius notalia* refers to *Belonella* sp. (Nesis 1979, 1987) and to *Taonius* sp. B of N Voss (personal communication). Examination of *Taonius* specimens including five *T. notalia*

Fig. 26 Specimen of *Taonius notalia* collected on a hook in the northwest of Crozet Islands (44°56’S, 44°47′E). Photos and copyright permission from N Servera

suggest that it is the single *Taonius* species that lives in subantarctic waters (Evans 2018). N Voss (personal communication) identified a *Taonius* collected in Crozet waters as being her *Taonius* species B, and a second whole specimen was recently recorded from the area (Fig. 26) (YC unpublished data). Additional *Taonius* catches within the Southern Ocean together with the occurrence of flesh and beaks in predators' stomach contents do indicate that *T. notalia* occurs commonly in the southern Atlantic, Indian, and Pacific Oceans, with some records from the Antarctic (Slip et al. 1995; Filippova 2002; Arata et al. 2004; Xavier et al. 2004, 2006; Xavier and Croxall 2005; Ceia et al. 2012; Cherel et al. 2017; Pereira et al. 2017; Mills et al. 2020). *Taonius notalia* was previously named *Taonius cymoctypus* (Imber 1978), *Taonius pavo* (Lubimova 1985; Rodhouse 1990; Filippova 2002), *Taonius* sp. (cf *pavo*) (Collins and Rodhouse 2006), and *Taonius* sp. B (Voss) (Xavier et al. 2018a). Mantle length to 46 cm but lower rostral length of accumulated beaks indicate that *T. notalia* can reach a larger size (YC unpublished data).

Beaks of *T. notalia* are illustrated in Clarke (1980 Text-fig 216) and Xavier and Cherel (2009). The genus *Taonius* has very distinctive beaks with, for example, their upper beaks being characterized by a long and thin curved rostrum (Imber 1978 Fig. 4; Xavier and Cherel 2009). Beaks from two *Taonius* taxa were identified from stomach contents of Southern Ocean predators, with *T. notalia* being the largest species (the smaller *T. expolitus* Evans, in prep occurs in subtropical waters; Evans 2018; YC unpublished data). It is likely that beaks from *T. notalia* and *T. expolitus* were pooled in some investigations, with large beaks indicating a predominance of the former species (as *Taonius* sp., Xavier et al. 2003a,b, 2006; *Taonius pavo*, Cooper et al. 1992). No studies yet refer to the recently described *T. notalia*, but its beaks were previously named *T. cymoctypus* (Berruti and Harcus 1978; Imber 1978 Figs. 4 and 5B; Berruti 1979; Imber and Berruti 1981; Thomas 1982; Schramm 1986), *Taonius* sp. (Rodhouse et al. 1987; Rodhouse 1990; Green and Burton 1993; Goldsworthy et al. 2002; Xavier et al. 2004), *Taonius* sp. (large) and *T. pavo* (small B) (Ridoux 1994), *T. pavo* (Imber 1976; Clarke 1980; Croxall and Prince 1980; Clarke et al. 1981; Clarke and MacLeod, 1982c; Rodhouse et al. 1987, 1990; Pascoe et al. 1990; Rodhouse 1990; Hunter and de L Brooke 1992; Clarke and Goodall 1994; Cooper and Klages 1995, 2009; Slip 1995; Slip et al. 1995; Clarke and Roper 1998; Field et al. 2007), *Taonius ?pavo* (Imber 1973; Imber and Russ 1975; Johnstone 1977), *T. pavo* (large type) (Green et al. 1998), *Taonius* cf. *pavo* (van den Hoff 2004), *Taonius* sp. (cf *pavo*) (Pilling et al. 2001; Xavier et al. 2002b; Arata and Xavier 2003; Arata et al. 2004), *Taonius* sp. B (Rodhouse et al. 1987; Rodhouse 1990; Imber 1992, 1999; James and Stahl 2000; van den Hoff 2001; Abreu et al. 2020), and *Taonius* sp. B (Voss) (Cherel et al. 2002c, 2004, 2011, 2017; Cherel and Duhamel 2004; Xavier and Cherel 2009; Delord et al. 2010; Xavier et al. 2011, 2014, 2018; Ceia et al. 2012; Connan et al. 2014; Alvito et al. 2015; Guerreiro et al. 2015; Pereira et al. 2017; Mills et al. 2020). Beaks from *T. notalia* are common in Southern Ocean predators' stomach contents and the species is an important food item of the Patagonian toothfish (Cherel et al. 2004), wandering albatross, southern royal albatross *Diomedea epomophora* (Forster, 1785) (Imber 1999; Xavier et al. 2003b), and southern bottlenose whale (Clarke and Goodall 1994).

***Todarodes filippovae* Adam, 1975** (Fig. 27): A circumpolar subantarctic and southern subtropical epi-mesopelagic species that extends northwards in the Peru Current (Alexeyev 1994a; Roeleveld 1989; Dunning 1998; Rodhouse 1998). *Todarodes filippovae* was originally described on the basis of specimens caught in subtropical waters of the Indian Ocean (Adam 1975). It was unfortunately synonymized afterwards with *T. angolensis* by K Nesis in 1979, but subsequent examination of additional specimens proved *T. filippovae* to be a valid species (Roeleveld 1989). Consequently, the literature, especially the Soviet/Russian literature, remains confused as to the identification and distribution of these two species (e.g., Vovk et al. 1978; Korzun et al. 1979; Nesis 1987). In addition, *T. filippovae* itself may comprise more than one species (Rodhouse 1998). Mantle length to 54 cm (Jereb and Roper 2010).

Three ommastrephid species occur within the Southern Ocean, *T. filippovae, T.* cf. *angolensis*, and *Martialia hyadesi. Martialia hyadesi* beaks can be differentiated from those of *Todarodes* (but they were previously named *Todarodes sagittatus* or *Todarodes ?sagittatus*, see above), while beaks from *T. filippovae* and *T.* cf. *angolensis* are so identical that they cannot be identified to the species level with confidence (Clarke 1986; Lu and Ickeringill 2002; Xavier and Cherel 2009). In addition, *Todarodes* beaks are also similar to those from the *Ommastrephes bartramii* complex that occurs north of the STF, thus complicating the picture for identifying accumulated ommastrephid beaks. To the best of my knowledge, *Todarodes filippovae* was not identified from the flesh in any stomach contents of Southern Ocean predators, except small juveniles (as *T. sagittatus*) that were probably the main squid prey of the northern rockhopper penguin *Eudyptes moseleyi* (Mathews & Iredale, 1921) from Gough Island (Klages et al. 1988). While fresh remains of *Todarodes* from Kerguelen predators refer to *T.* cf. *angolensis* (see below), it is likely that the few *Todarodes* and ommastrephid beaks found in the Southern Ocean outside the Kerguelen area refer mostly to *T. filippovae* (Berruti and Harcus 1978; Imber and Berruti 1981; Imber 1999; Clarke 1980; Clarke and MacLeod 1982c; Rodhouse 1990; Ridoux 1994; Clarke and Roper 1998; Xavier et al. 2004, 2006; Xavier and Croxall 2005; Mills et al. 2020).

Fig. 27 Specimens of *Todarodes filippovae* (left) and *T.* cf. *angolensis* (right) collected over the Chatham Rise (New Zealand) and in New Zealand subantarctic waters, respectively. Photo and copyright permission from D Stevens

***Todarodes* cf. *angolensis* Adam, 1962** (Fig. 27): A presumably shelf and slope, and oceanic epi-mesopelagic circumpolar endemic (YC unpublished data). Based on the number of teeth on the medial manus sucker rings, *T.* cf. *angolensis* occurs in the southern Tasman Sea (Dunning 1998, Dunning and Wormuth 1998), and in Kerguelen waters (Cherel and Weimerskirch 1995; Cherel et al. 2004). *Todarodes* cf. *angolensis* was initially named *T. angolensis* (Cherel and Weimerskirch 1995; Dunning 1998, Dunning and Wormuth 1998, Cherel et al. 2000a; Cipro et al. 2018), but its taxonomic status needs further morphological and genetic investigations, because *T. angolensis* was described from specimens caught in the distant subtropical waters of southern Africa (Adam 1962). *Todarodes* cf. *angolensis* occurs in both the Indian and Pacific Oceans, and it was not yet recorded in the Atlantic Ocean, probably due to confusion with *T. filippovae* (see above). Both fishery bycatch and predators' diet indicate that *T.* cf. *angolensis* outnumbers the two other ommastrephids occurring in Kerguelen waters, namely *T. filippovae* and *Martialia hyadesi* (Piatkowski et al. 1991; YC unpublished data). The largest collected *T.* cf. *angolensis* at Kerguelen Islands had a ML of 46 cm (YC unpublished data); mantle length to 59 cm in the Tasman Sea (Dunning 1998).

Since two distinct species of *Todarodes* with similar beaks occur at Kerguelen Islands, beaks were named *Todarodes* sp. (Cherel and Weimerskirch 1995; Cherel et al. 2000a,b, 2002c, 2004, 2008, 2017; Cherel and Hobson 2005; Xavier and Cherel 2009; Delord et al. 2010). However, the predominance of *T.* cf. *angolensis* over *T. filippovae* in Kerguelen waters strongly suggests that most *Todarodes* sp. are *T.* cf. *angolensis*. Juveniles of that abundant species are important cephalopod prey of porbeagle sharks *Lamna nasus*

(Bonnaterre, 1788), and of black-browed and gray-headed albatrosses (Cherel et al. 2000b, 2002c; Cherel and Duhamel 2004).

Regional subantarctic species

***Doryteuthis gahi* (d'Orbigny, 1835)**: A neritic and slope southern South America endemic from southern Peru to northern Argentina (Jereb and Roper 2010; Tolweb 2019). The species is abundant near the Falkland Islands and supports an important fishery on the Patagonian shelf (Hatfield and Rodhouse 1991). *Doryteuthis gahi* was formerly named *Loligo gahi* (Anderson 2000) and *L. patagonica* is a junior synonym of *D. gahi* (Nesis 1987; Brakoniecki 1984). It is the single myopsid squid living within the Southern Ocean. Mantle length to 28 cm (Tolweb 2019).

Beaks of *D. gahi* were illustrated in Xavier and Cherel (2009). They were previously named *Loligo* sp. (Rodhouse et al. 1987; Copello et al. 2008). Beaks and fresh remains of *D. gahi* (as *Loligo gahi*) were recorded in the diet of many predators from the southwestern Atlantic Ocean. They include commercial fishes, penguins, albatrosses, and marine mammals (Alonso et al. 2000; Jackson et al. 2000a; Arata and Xavier 2003; Laptikhovsky et al. 2010; Scioscia et al. 2014; Handley et al. 2016). For example, *D. gahi* is the most common cephalopod prey of long-finned pilot whales *Globicephala melas edwardii* (Traill, 1809) and of Commerson's dolphins *Cephalorhynchus commersonnii* Lacépède, 1804, in Tierra del Fuego (Clarke and Goodall 1994). In the Falkland Islands, black-browed albatrosses scavenge waste generated by the squid fishery, including fish and *D. gahi* (Thompson 1992).

***Enoploteuthis semilineata* Alexeyev, 1994**: A poorly known southern subtropical and northern subantarctic epipelagic species from the southern Pacific Ocean (Alexeyev 1994a,b). *Enoploteuthis lineata* was not recorded in the scientific literature since its original description from eight specimens caught with commercial pelagic trawls in the vicinity of the STF (Alexeyev 1994a,b, but see Laptikhovsky et al. 2017). It was named *Enoploteuthis* sp. (Alexeyev 1994a). Mantle length to 8.9 cm (Alexeyev 1994b).

To the best of my knowledge, neither photos nor drawings of the beaks from *E. lineata* were published. This, together with its restricted biogeographical range and the paucity of records explain why *E. lineata* was not reported in any dietary studies of Southern Ocean predators.

***Illex argentinus* (Castellanos, 1960)**: A neritic and slope epi-mesopelagic endemic to the western Atlantic from southern Brazil to southern Argentina and the Falkland Islands, which occurs occasionally south to the PF (Rodhouse 1991, Roper et al. 1998; Jereb and Roper 2010). Surprisingly, *I. argentinus* was not listed in the Southern Ocean teuthofauna (Collins and Rodhouse 2006; Rodhouse et al. 2014), while it is extremely abundant and supports a major international fishery in subantarctic waters off Argentina and the Falklands (Waluda et al. 2008; Jereb and Roper 2010). Due to its commercial importance, the species was studied intensively and is one of the best known oegopsid squids (Jereb and Roper 2010). Mantle length to 40 cm (Nesis 1987).

Beaks of *I. argentinus* were illustrated in Xavier and Cherel (2009). They were previously named *Illex* sp. (Rodhouse et al. 1987; Rodhouse 1989, 1990). The species is an important component of the Brazilian and Patagonian shelf ecosystems both as a predator and a prey (dos Santos and Haimovici 2000; Jereb and Roper 2010; Arkhipkin 2013). Accordingly, *I. argentinus* was found in the diet of albatrosses, petrels, pinnipeds, and odontocetes from Patagonia, the Falkland Islands, and South Georgia (Rodhouse et al. 1987; Thompson 1992; Berrow and Croxall 1999; Alonso et al. 1999, 2000; Xavier et al. 2002a; Copello et al. 2008). However, it is uncertain where and how *I. argentinus* is taken by predators, whether caught naturally or during fishery operations. Within that context, it is noticeable that the species was found in the diet of fish and seabirds outside its geographical range, where *I. argentinus* is commonly used as bait by longliners targeting the Patagonian toothfish (Catard et al. 2000; Cherel et al. 2004, 2017).

***Notonykia nesisi* Bolstad, 2007**: An epi-mesopelagic endemic from subantarctic waters of New Zealand and Australia that occurs south to the SAF (Bolstad 2007; Atlas of Living Australia 2020). The species is closely related to the second species in the genus *Notonykia*, *N. africanae* (Bolstad 2007). *Notonykia nesisi* was previously named *Ancistroteuthis lichtensteinii* Pacific form (Kubodera et al. 1998; see also Nesis et al. 1998b). It was not previously listed in the Southern Ocean teuthofauna (Rodhouse et al. 2014). Maximum known mantle length 11 cm, but mature animals are unknown (Bolstad 2007, 2010).

Drawings of the lower beak of *N. nesisi* were included in the species description (Bolstad 2007, 2010). A thorough examination of its beaks together with a comparison with those from *N. africanae* is needed to preclude confusion between the two *Notonykia* species in the Pacific Ocean. *Notonykia*

Fig. 28 Specimen of *Nototodarus sloanii* collected over the Chatham Rise (New Zealand). Photo and copyright permission from D Stevens

nesisi was not reported in any dietary studies of Southern Ocean predators.

***Nototodarus sloanii* (Gray, 1849)** (Fig. 28): A neritic and slope epi-mesopelagic endemic from subantarctic and STF waters of New Zealand that occurs south to the SAF (Smith et al. 1987; Dunning and Förch 1998). *Nototodarus sloanii* was not listed in the Southern Ocean teuthofauna (Collins and Rodhouse 2006; Rodhouse et al. 2014), while it forms the basis for major international demersal trawl and jig fisheries in subantarctic New Zealand (Jereb and Roper 2010). The species was previously named *Nototodarus* sp. (Nesis 1987). Mantle length to 42 cm (Smith et al. 1987).

Beaks of *N. sloanii* were illustrated in Clarke (1986). Ommastrephid beaks are notably difficult to identify to the genus and species levels (Clarke 1986), thus probably explaining why beaks referring to *Nototodarus* were erroneously identified in the diet of sooty albatrosses from Marion Island (Berruti and Harcus 1978; Imber and Berruti 1981) and of Adélie penguins *Pygoscelis adeliae* (Hombron and Jacquinot, 1841) from the Ross Sea (Emison 1968). They were previously named type Bii beaks (Gaskin and Cawthorn 1967a,b), *Nototodarus* sp. (West and Imber 1986; van Heezik 1990; Imber 1991; James and Stahl 2000), and *Nototodarus sloani sloani* (Imber 1976). Two *Nototodarus* species occur in New Zealand waters, *N. gouldi* in the north and *N. sloanii* in the south (Smith et al. 1987). It is likely that the latter predominates in the diet of subantarctic predators and, indeed, *N. sloanii* is a significant prey item of penguins, albatrosses, and otariids (van Heezik 1990; Imber 1999; Waugh et al. 1999; James and Stahl 2000; Meynier et al. 2009; Flemming et al. 2013; Lalas and Webster 2014). Since it is used as bait by longliners, *N. sloanii* was recently found in stomach contents outside its geographical range in Antarctic waters (Roberts et al. 2011).

***Octopoteuthis fenestra* Kelly, in prep** (as cited in Kelly 2019) (Fig. 29): A meso-bathypelagic endemic from subantarctic waters of New Zealand and Australia that occurs in the vicinity of the STF. This recently described species is the most southerly distributed *Octopoteuthis* (Kelly 2019). Mantle length to 23 cm (Kelly 2019).

Fig. 29 Specimen of *Octopoteuthis fenestra* collected over the Chatham Rise (New Zealand). Photo and copyright permission from D Stevens

Beaks of *O. fenestra* were illustrated in Kelly (2019). They look similar to those of other small-sized *Octopoteuthis*, including *O. rugosa*, which has a circumpolar distribution within the STZ. Hence, the two species overlaps in the STF waters of the western Pacific (Kelly 2019). *Octopoteuthis* beaks were found in the diet of Southern Ocean predators, but mostly as accumulated items (e.g., Cherel et al. 2017), thus suggesting that squids were caught outside the Southern Ocean. However, flesh was found in sperm whales caught at 47°S, thus indicating the presence of *Octopoteuthis* within the SAZ of the Tasman Sea (Clarke and MacLeod 1982c). In many cases, *Octopoteuthis* beak measurements indicate the occurrence of two to three size classes, including both the giant *Octopoteuthis* form and smaller form(s) like *O. fenestra* and *Octopoteuthis rugosa*. No dietary studies yet refer to the recently described *O. fenestra*.

***Ommastrephes cylindraceus* d'Orbigny, 1835**: An Indo-Atlantic southern subtropical epi-mesopelagic species that occurs in subantarctic waters south to ~46°S–55°S in the western Atlantic (Korzun et al. 1979; Jereb and Roper 2010; Fernandez-Alvarez 2018). *Ommastrephes cylindraceus* is one of the four species that form the *Ommastrephes bartramii* complex, which also includes *O. brevimanus* in the southern subtropical Pacific Ocean (Fernandez-Alvarez 2018). Mantle length to 90 cm and body mass to 25 kg (Fernandez-Alvarez 2018).

Ommastrephes beaks are illustrated in Clarke (1986) and Lu and Ickeringill (2002). They are pretty similar to those from *Todarodes* species, thus complicating their identification. Two lower beaks of *O. cylindraceus* (as *O. bartramii*) were found in the diet of king penguins from the Falkland Islands (Piatkowski et al. 2001), and fresh items were identified in the diet of sperm whales in the southern Atlantic (Vovk et al. 1978).

***Promachoteuthis* sp. B Roper & Young, 1968**: Known from four small specimens collected in subantarctic (56–57°S) and southern subtropical (33–34°S) waters of the Pacific Ocean (Voss 1992; Tolweb 2019). Possibly occurs in the North Atlantic (Tolweb 2019). Adult size unknown (Tolweb 2019).

Drawings of the beaks are available (Roper and Young 1968) but *Promachoteuthis* sp. B was not recorded in the diet of Southern Ocean predators.

Occasional subantarctic species

***Abraliopsis gilchristi* (Robson, 1924)**: A circumglobal southern subtropical epipelagic species that was found south of the STF in the Pacific Ocean and occasionally in the Indian Ocean (Nesis 1987; Alexeyev 1994a; Cherel et al. 2011). Mantle length to 5.7 cm (Alexeyev 1994a).

Beaks of *A. gilchristi* were illustrated in Lu and Ickeringill (2002). Accumulated beaks of *A. gilchristi* (as *Abraliopsis ?gilchristi*) were reported in a single dietary study that detailed the prey items of the black petrel (Imber 1976).

***Ancistrocheirus lesueurii* (d'Orbigny, 1842)**: A cosmopolitan subtropical and tropical epi-mesopelagic species reaching subantarctic waters (Nesis 1987; Alexeyev 1994a). *Ancistrocheirus alessandrini* is a junior synonym of *A. lesueurii* (Bello 1992). Mantle length to 54 cm (Hoving and Lipinski 2015).

The typical lower beaks of *A. lesueurii* were well illustrated (Clarke 1980, 1986; Lu and Ickeringill 2002; Xavier and Cherel 2009). They were misidentified as *Mastigoteuthis* sp. B (Imber and Russ 1975, details in Imber 1992). *Ancistrocheirus lesueurii* beaks are commonly found as accumulated items in the diet of highly mobile Southern Ocean predators like albatrosses (e.g., Xavier et al. 2003b, 2014; Cherel et al. 2017). This suggests that most *A. lesueurii* were caught in subtropical waters, with the lack of fresh remains indicating it occurs rarely within the Southern Ocean (but see Clarke and Prince 1981).

***Chiroteuthis joubini* Voss, 1967**: An Atlantic and Indian tropical and subtropical mesopelagic species that occurs occasionally in subantarctic waters (Nesis and Nikitina 1984; Nesis 1987; Tolweb 2019). *Chiroteuthis joubini* was rarely recorded in temperate waters of the Southern Hemisphere (Clarke 1980), but one specimen was collected north of the Kerguelen Islands at 45°S, within the SAZ (Nesis and Nikitina 1984). Mantle length to 25 cm, possibly up to 50 cm (Nesis 1987).

Beaks of *C. joubini* were illustrated in Clarke (1980, 1986), with its lower beaks looking like large beaks of *C. mega*. They were named *Chiroteuthis* sp. A (Clarke 1980; Rodhouse et al. 1987; Rodhouse 1990; details in Clarke et al. 1993) and were misidentified as *C. veranyi* (Berruti and Harcus 1978; Imber and Berruti 1981; Schramm 1986). *Chiroteuthis joubini* is a rare prey species of Southern Ocean seabirds and always as accumulated items (Rodhouse et al. 1987), with some identifications requiring confirmation (Imber 1973, 1976; Clarke and MacLeod 1982b; Green et al. 1998). However, both fresh and accumulated items were found in the diet of sperm whales caught in adjacent subtropical waters of the western and eastern Indian Ocean (Clarke 1980).

***Chiroteuthis mega* (Joubin, 1932)**: A subtropical meso-bathypelagic species that occurs occasionally in subantarctic waters (Tolweb 2019; this study). *Chiropsis* is a junior synonym of *Chiroteuthis* (Tolweb 2019) and *C. capensis* a junior synonym of *C. mega* (Salcedo-Vargas 1997). *Chiroteuthis mega* was recorded from the north and south Atlantic and Pacific oceans. However, two typical upper beaks were identified from stomach contents of Patagonian toothfish caught at the Crozet Islands (Cherel et al. 2004), thus indicating that *C. mega* also occurs in the Indian Ocean and occasionally in subantarctic waters (Laptikhovsky et al. 2017). Mantle length to 21 cm (Mensch 2010; Shea et al. 2017).

Examination of beaks from a specimen from New Zealand synonymized *Chiroteuthis* sp. F (Imber) with *C. mega*. *Chiroteuthis* sp. F was firstly described from beaks found in stomach contents of albatrosses and poorly illustrated (Imber 1992). Beaks from *Chiroteuthis* sp. F were subsequently identified in small numbers in several dietary investigations (Imber 1999; Cherel et al. 2004, 2017; Xavier et al. 2014; Beasley et al. 2019). *Chiroteuthis mega* is a rare prey species of Southern Ocean seabirds and always as accumulated items (Imber 1992; Xavier et al. 2014).

***Cycloteuthis sirventi* Joubin, 1919**: A cosmopolitan tropical and subtropical epi-mesopelagic species that occurs occasionally in subantarctic waters (Jereb and Roper 2010). *Cycloteuthis akimushkini* is a junior synonym of *C. sirventi* (Filippova 1968; Clarke et al. 1993; Tolweb 2019). The species was identified from the flesh in the diet of sperm whales in the Southern Ocean as *Cycloteuthis* sp. (Mikhalev et al. 1981) and *C. akimushkini* (Vovk et al. 1978). Mantle length to 60 cm (Jereb and Roper 2010).

The typical lower beak of *C. sirventi* is well described and illustrated (Filippova 1968; Clarke 1980 Text-fig 163, 1986; Xavier and Cherel 2009). Beaks of *C. sirventi* ware named *C. akimushkini* in most dietary investigations (Clarke 1980, 1986; Clarke and MacLeod 1982c; Cooper et al. 1992; Imber 1992, 1999; Cherel and Weimerskirch 1999; Cherel and Duhamel 2004; Cherel et al. 2004, 2011; Xavier and Cherel 2009; Xavier et al. 2011, 2014; Connan et al. 2014; Guerreiro et al. 2015). They were also called *Cycloteuthis ?akimushkini* (Imber 1973, 1976; Imber and Russ 1975) and *Cycloteuthis* sp. (Ridoux 1994; Cooper and Klages 1995, 2009). Accumulated beaks from *C. sirventi* were identified in stomach contents of Southern Ocean predators, including albatrosses and sperm whales (e.g., Clarke 1980; Xavier et al. 2014; Cherel et al. 2017). One and 11 beaks with no flesh attached were found in one and five stomach contents of southern sleeper sharks, thus showing the species occurs in Kerguelen and Crozet waters, respectively (Cherel and Duhamel 2004).

***Dosidicus gigas* (d'Orbigny, 1835)**: An eastern Pacific tropical and subtropical nerito-oceanic epi-mesopelagic species that invades occasionally subantarctic waters of Chile (Nesis 1987; Nigmatullin et al. 2001). The jumbo squid is an important commercially exploited squid that recently expanded its range in latitudes and unusually occurred south to 53°S, approaching Tierra del Fuego (Jereb and Roper 2010; Ibanez et al. 2015). *Dosidicus gigas* is the largest ommastrephid with a mantle length to 120 cm and a body mass of up to 50 kg (Nigmatullin et al. 2001).

Beaks of *D. gigas* are easy to distinguish from those of other ommastrephids by their overall large size and size at darkening (Clarke 1986). Neither flesh nor accumulated beaks of *D. gigas* were reported in dietary studies of Southern Ocean predators.

Histioteuthis macrohista **Voss, 1969**: A circumglobal southern subtropical meso-bathypelagic species that occurs occasionally in fringing subantarctic waters (Voss et al. 1998). *Histioteuthis macrohista* was listed as a subantarctic histioteuthid (Voss 1969; Nesis 1987) but the paucity of its records south of the STF (Laptikhovsky et al. 2017) suggests it is an occasional species there. An almost intact specimen was found in a stomach content of king penguin, thus indicating it was caught close to the Crozet Islands (Cherel et al. 1996). Mantle length to 7.5 cm (Reid 2016).

Beaks of *H. macrohista* are well illustrated (Clarke 1980 Text-fig 183, 1986; Lu and Ickeringill 2002, Xavier and Cherel 2009). According to its morphological features, the lower beak of *H. macrohista* belongs to the type A of histioteuthid beaks and corresponds to beak type A1 (Clarke 1980, 1986). It was named *Histioteuthis ?macrohista* (Imber and Russ 1975), misidentified as *H. ?meleagroteuthis* (Clarke 1980; Clarke and Prince 1981; Clarke and MacLeod 1982c), and it was sometimes not differentiated from other type A beaks (Rodhouse et al. 1987; Rodhouse et al. 1990; Ridoux 1994; Green et al. 1998; Xavier et al. 2003b; Xavier and Croxall 2007). *Histioteuthis macrohista* beaks were regularly found in small numbers as accumulated items in the diet of Southern Ocean predators (e.g., Clarke 1980; Imber 1992, 1999; Xavier et al. 2014).

Histioteuthis miranda **(Berry 1918)**: A southern subtropical and tropical epi-mesopelagic and slope species that occurs occasionally south of the STF (Filippova 1972); *Histioteuthis miranda* ranges from western Southern Africa eastwards to the western Pacific Ocean (Voss et al. 1998). The species was rarely caught south of the STF in New Zealand waters (Voss et al. 1998), and fresh remains from a few specimens were found in stomach contents of wandering albatrosses breeding in South Georgia and at the Crozet Islands (Xavier et al. 2004, 2006; Xavier and Croxall 2005; Cherel et al. 2017; Pereira et al. 2017). Hence, *H. miranda* is not a “notalian” species (Braid and Bolstad 2019). Mantle length to 29 cm (Hoving and Lipinski 2009).

Beaks of *H. miranda* are well illustrated (Clarke 1980, 1986; Lu and Ickeringill 2002; Xavier and Cherel 2009). According to its morphological features, the lower beak of *H. miranda* belongs to the type A of histioteuthid beaks and corresponds to beak type A3 (Clarke 1980, 1986; Clarke et al. 1993). It was named *Histioteuthis ?miranda* (Imber and Russ 1975) and sometimes not differentiated from other type A beaks (Rodhouse et al. 1987; Rodhouse et al. 1990; Ridoux 1994; Green et al. 1998; Xavier et al. 2003b; Xavier and Croxall 2007). *Histioteuthis miranda* beaks were regularly found in small numbers as accumulated items in the diet of Southern Ocean predators (e.g., Clarke 1980; Cooper et al. 1992; Cooper and Klages 1995; Imber 1992, 1999; Xavier et al. 2014).

Magnoteuthis osheai **Braid & Bolstad, 2015**: Probably a circumglobal southern subtropical meso-bathypelagic species that occurs occasionally in subantarctic waters (Braid and Bolstad 2015; this study). *Magnoteuthis osheai* was recently described from nine specimens collected in subtropical waters off New Zealand, and it is possible that *Magnoteuthis* type beta (Tolweb 2019) and *M. osheai* are the same species (Braid and Bolstad 2015). The single specimen of *Magnoteuthis* type beta was collected in subantarctic waters south of New Zealand (Tolweb 2019). Beaks of *M. osheai* collected from seabirds’ diets added 31 records, thus indicating that the species occurs not only in the southern Pacific but also in the southern Indian and Atlantic Oceans (Table 4). Mantle length to 18 cm (Braid and Bolstad 2015), but lower rostral length of accumulated beaks indicate *M. osheai* reaches a larger size (Table 3).

Drawings of beaks of *M. osheai* were included in the species description (Braid and Bolstad 2015). A recent examination revealed that beaks of *M. osheai* are identical to those previously named *Mastigoteuthis* sp. A by M Imber (YC unpublished data). They were identified as rare accumulated items in the diet of Southern Ocean albatrosses (Imber 1976, 1992, 1999; Imber and Berruti 1981; Xavier et al. 2014; Cherel et al. 2017) (Table 4). Importantly, beaks named *Mastigoteuthis* sp. A (Imber) differ from those named *Mastigoteuthis* sp. A by MR Clarke (Prince 1980b; Clarke et al. 1981; Rodhouse et al. 1987; Pascoe et al. 1990; Rodhouse 1990; Ridoux 1994), which refers today to *Asperoteuthis lui* (see above).

Megalocranchia maxima **Pfeffer, 1884**: An Atlantic and western Indian Ocean southern subtropical meso-bathypelagic species that also occurs in the Pacific Ocean (Jereb and Roper 2010; Evans 2018). Identification of species within the genus *Megalocranchia* is challenging and requires a taxonomic revision worldwide (Evans 2018). *Megalocranchia maxima* was mapped in subantarctic waters (Jereb and Roper 2010), but the lack of subantarctic records of *Megalocranchia* in the literature suggests that its occurrence within the Southern Ocean is rare. One upper beak of *Megalocranchia* sp. was found in the stomach content of a southern sleeper shark caught in Kerguelen waters (Cherel and Duhamel 2004). Mantle length to 180 cm (Jereb and Roper 2010).

Beaks of *Megalocranchia* sp. are well illustrated and they were initially named *Phasmatopsis cymoctypus* (Clarke 1980; Clarke and Roper 1998, details in Clarke 1986) and Oegopsida sp. C (Cherel and Duhamel 2004). Accumulated beaks of *Megalocranchia* sp. are uncommon to very rare prey items of Southern Ocean predators, including sperm whales (Clarke 1980) and albatrosses (Rodhouse et al. 1987; YC unpublished data).

Teuthowenia pellucida **(Chun, 1910)** (Fig. 30): A circumglobal southern subtropical epi-meso-bathypelagic

Table 4 Records of the mastigoteuthid *Magnoteuthis osheai* as accumulated beaks in predators' stomach contents and comparison with the largest known specimen

Location	Initial identification	Samplers	Sampling years	Items	Number of specimens	Lower rostral length (mm)	References
Atlantic Ocean							
Gough	*Mastigoteuthis* sp. A (Imber)	Tristan albatross	1979	Four lower beaks	4	No data	Imber (1992)
Indian Ocean							
Marion Island	*Mastigoteuthis* sp. A (Imber)	Wandering albatross	1974, 1979	Two lower beaks	2	No data	Imber and Berruti (1981); Imber (1992)
Kerguelen Islands	*Mastigoteuthis* sp. A (Imber)	Wandering albatross	1998	Five lower and two upper beaks	5	5.0–5.6	Cherel et al. (2017)
Amsterdam Island	*Mastigoteuthis* sp. A (Imber)	Indian yellow-nosed albatross	1993, 2001	Three lower and four upper beaks	4	4.8–5.8	Cherel, unpublished data
Pacific Ocean							
New Zealand	*Mastigoteuthis* sp. A (Imber)	Northern royal albatross	1981–1996	Two lower beaks	2	No data	Imber (1999)
	Mastigoteuthis (three species)	Gray-faced petrel	1971	At least one lower beak	1	5.1	Imber (1973); personal communication
Chatham Islands	*Mastigoteuthis* sp. A (Imber)	Northern royal albatross	1973–1983	Three lower beaks	3	No data	Imber (1999)
Auckland Islands	*Mastigoteuthis* sp. A (Imber)	Gibson's albatross	2001	One lower beak	1	5.7	Xavier et al. (2014); personal communication
Antipodes Island	*Mastigoteuthis* sp. A (Imber)	Antipodean albatross	1978	Five lower beaks	5	4.7–5.2	Imber (1992)
	Mastigoteuthis sp. A (Imber)	Antipodean albatross	2001	three lower beaks	3	5.1–5.5	Xavier et al. (2014); personal communication
Campbell Island	*Mastigoteuthis* sp. A (Imber)	Southern royal albatross	1974–1997	One lower beak	1	No data	Imber (1999)
Total					31		
New Zealand	*Magnoteuthis osheai*	trawl	2010	Largest specimen (18 cm ML)	1	4.8	Braid and Bolstad (2015)

Abbreviation: *ML* mantle length

Fig. 30 Specimen of *Teuthowenia pellucida* collected over the Chatham Rise (New Zealand). Photo and copyright permission from D Stevens

species that occurs occasionally in subantarctic waters (Voss 1985). *Teuthowenia pellucida* was considered as a subantarctic-southern subtropical species (Nesis 1987), but the peaucity of records indicate it rarely occurs south of the STF (Voss 1985; Alexeyev 1994a). *Teuthowenia richardsoni* is a junior synonym of *T. pellucida* (Voss 1985; Nesis 1987). A closely related species (*T.* aff. *pellucida*) occurs in northern New Zealand waters (Braid and Bolstad 2019). Mantle length to 21 cm (Evans and Bolstad 2015).

Nice drawings of *T. pellucida* beaks were included in the species re-description (Voss 1985). They were also illustrated in Lu and Ickeringill (2002) and Xavier and Cherel (2009). The lower beak of *T. pellucida* was named *Fusocranchia pellucida* (Imber 1978), *Megalocranchia pardus* (Imber 1976), *Megalocranchia richardsoni* (Imber 1973, 1976; Imber and Russ 1975), *Teuthowenia* sp. (van den Hoff 2001), *Teuthowenia megalops impennis* (Berruti and Harcus 1978; Imber 1978 Fig. 6D; Imber and Berruti 1981; Schramm 1986), *Teuthowenia impennis* (West and Imber 1986), *Teuthowenia* or *Galiteuthis* type B beak (Clarke and MacLeod 1982c; Clarke 1986; details in Voss 1985), and *Galiteuthis* sp. (Rodhouse et al. 1987; Rodhouse 1990). Small numbers of accumulated beaks of *T. pellucida* were found in stomach contents of Southern Ocean albatrosses (Imber 1992, 1999; James and Stahl 2000; Xavier et al. 2014; Cherel et al. 2017) and one pair of its beaks was identified from the stomach content of a Patagonian toothfish caught in Kerguelen waters (Cherel et al. 2004).

***Walvisteuthis rancureli* (Okutani, 1981)**: A circumglobal southern subtropical and tropical meso-bathypelagic species that occurs occasionally in subantarctic waters (Kubodera et al. 1998; Bolstad 2010; this study). *Walvisteuthis rancureli* was described as *Onykia rancureli* (Okutani 1981) and subsequently called *Callimachus rancureli* (Bolstad 2010). Some authors synonymized *W. rancureli* with *Walvisteuthis virilis* (Jereb and Roper 2010; Reid 2016). Mantle length to 15 cm (Tolweb 2019).

An unknown lower beak of onychoteuthid was firstly poorly described as *Onychoteuthis* sp. C (Imber 1992) before a thorough examination of beaks synonymized the species with *W. rancureli* (YC unpublished data). Beaks sorted from intact specimens of *W. rancureli* found in the diet of large tropical fishes (6.2–8.6 cm ML) were smaller than those found in the diet of Southern Ocean predators, which is in agreement with mature individuals reaching a larger size. Beaks from the three other species of *Walvisteuthis* (Tolweb 2019) were not examined, including those from the southern subtropical *W. virilis* (Nesis and Nikitina 1992), thus precluding a definite identification of the beaks at the species level. Beaks from *W. rancureli* were named *Onychoteuthis* sp. C (Imber 1992, 1999; Cherel and Weimerskirch 1999; Cherel et al. 2004, 2017) and misidentified as those from *Onychoteuthis banksi* (Clarke et al. 1981; Rodhouse et al. 1987; Rodhouse 1990, details in Imber 1992). *Walvisteuthis rancureli* is an uncommon prey item of Southern Ocean albatrosses (Imber 1992, 1999; Cherel et al. 2017). In agreement with the hypothesis that *Onychoteuthis* sp. C lives as far south as the PF (Imber 1992), two lower beaks of *W. rancureli* were identified in the diet of Patagonian toothfish from the Crozet Islands (Cherel et al. 2004).

Doubtful taxa and records

Chiroteuthidae Genus C, new? Richard & Roper, 2017: A single badly damaged brachial crown was collected in Antarctic waters south of South America (Tolweb 2019). Chiroteuthidae new genus C is probably a junior synonym of *A. lui* (Braid 2017), but it was also hypothesized to be another species of *Asperoteuthis* or *B. skolops* (Tolweb 2019).

Examination of the specimen's beaks could help disentangling the taxonomy, because beaks of *A. lui* and *B. skolops* are morphologically different (Xavier and Cherel 2009). Chiroteuthidae new genus C was not reported in the diet of Southern Ocean predators.

***Histioteuthis bonnellii corpuscula* Clarke, 1980**: A circumpolar southern subtropical meso-bathypelagic species (Voss et al. 1998). The taxonomic status of *H. bonnellii corpuscula* needs further investigation. The subspecies was first described from specimens caught off South Africa (Clarke 1980), but it was afterwards united to *H. bonnellii bonnellii* to form a single species, *H. bonnellii* (Voss et al. 1998). However, several important features suggest that *H. bonnellii corpuscula* differentiates from *H. bonnellii bonnellii* at the species level: (i) its lower beak is distinctive, being different in size and morphology to that of *H. bonnellii bonnellii* (Clarke 1980, 1986; Clarke et al. 1993); (ii) *H. bonnellii corpuscula* grows to a smaller size than *H. bonnellii bonnellii* (Clarke 1980); (iii) their biogeography does not overlap, with *H. bonnellii bonnellii* occurring further north in the Atlantic than *H. bonnellii corpuscula*, and the latter living also in the southern Indian and Pacific Oceans (Voss et al. 1998); and (iv) a recent DNA analysis verified the initial hypothesis of genetic isolation (Clarke 1980) by assigning different barcode index numbers to north Atlantic (*H. bonnellii*) and New Zealand (*H.* aff. *bonnellii*) specimens (Braid and Bolstad 2019). Jereb and Roper (2010) mapped *H. bonnellii corpuscula* in northern subantarctic waters, but its southern limit appears more likely to be the STF (Voss et al. 1998). Accordingly, fresh remains of that species were not recorded from dietary analysis of Southern Ocean predators. Hence, the occurrence of *H. bonnellii corpuscula* within the Southern Ocean is doubtful. Mantle length to 9.0 cm (Nesis 1987).

Beaks of *H. bonnellii corpuscula* were well illustrated (Clarke 1980, 1986; Lu and Ickeringill 2002; Xavier and Cherel 2009). According to its morphological features, the lower beak of *H. bonnellii corpuscula* belongs to the type A of histioteuthid beaks and corresponds to beak type A2 (Clarke 1980, 1986; Clarke et al. 1993). It was sometimes not differentiated from other type A beaks (Rodhouse et al. 1987, 1990, Ridoux 1994; Green et al. 1998; Xavier et al. 2003b; Xavier and Croxall 2007). *Histioteuthis bonnellii corpuscula* beaks were named *H. bonnellii* (Clarke et al. 1981), *H. ?bonnellii* (Imber 1973), *H. corpuscula* (Mills et al. 2020), and they were misidentified as *H. ?atlantica* (Imber and Russ 1975) and *H. meleagroteuthis* (Berruti and Harcus 1978; Berruti 1979; Imber and Berruti 1981; Thomas 1982; Schramm 1986). Accumulated beaks of the species were identified from stomach contents of albatrosses that are known to forage both within and north of the Southern Ocean, with *H. bonnellii corpuscula* being likely caught within the STZ (e.g., Imber 1992; Xavier et al. 2014).

***Histioteuthis corona* (Voss & Voss, 1962)**: A tropical and subtropical meso-bathypelagic species/subspecies group (Voss et al. 1998; Tolweb 2019). Nesis (1987) indicated that the group extends to subantarctic waters between the Bounty and Antipodes Islands. However, a detailed investigation by Voss et al. (1998) gave no indication of specimens from the *H. corona* group south of the STF. Hence, their presence within the Southern Ocean is doubtful and requires more sampling in subantarctic waters south of New Zealand. Mantle length to 17 cm (Tolweb 2019).

The lower beak of *H. corona* was illustrated in Clarke (1986). Beaks from the *H. corona* group were not recorded in the diet of any Southern Ocean predator.

***Lepidoteuthis grimaldii* Joubin, 1895**:A cosmopolitan tropical and subtropical meso-bathypelagic species (Jereb and Roper 2010). *Lepidoteuthis grimaldii* was reported to reach subantarctic waters in the Atlantic Ocean (Nesis 1987), but no recent records of the species occurred south of the STF and consequently the occurrence of *L. grimaldii* within the Southern Ocean is doubtful (but see Jackson and O'Shea 2003). Mantle length to 100 cm (Nesis 1987).

Lepidoteuthis grimaldii was first described from three incomplete specimens recovered from the stomachs of sperm whales and Risso's dolphins *Grampus griseus* (Cuvier, 1812) (Clarke and Maul 1962). Beaks of *L. grimaldii* were well described and photographed (Clarke and Maul 1962; Clarke 1980, 1986; Lu and Ickeringill 2002; Xavier and Cherel 2009; Escanez et al. 2017) but its lower beak can be confused with those from *T. danae* and from the giant *Octopoteuthis* forms that have an overall similar shape (Clarke 1986). Beaks of *L. grimaldii* were named *Lepidoteuthis* sp. (Ridoux 1994), *Lepidoteuthis ?grimaldii* (Imber 1999) and beak type D (Gaskin and Cawthorn 1967a,b). They were found as accumulated items in the diet of some Southern Ocean predators, including sperm whales (Clarke 1980) and albatrosses (Imber 1992; Xavier et al. 2003b; Cherel et al. 2017).

***Pyroteuthis margaritifera* (Rüppell, 1844)**: A cosmopolitan tropical and subtropical epi-mesopelagic species (Nesis 1987). It was assumed that *P. margaritifera* occurs in subantarctic waters of the Pacific Ocean (Jereb and Roper 2010), but Alexeyev (1994a) wrote that the species "practically does not penetrate subantarctic waters." Hence, the occurrence of *P. margaritifera* within the Southern Ocean is doubtful. Mantle length to 5.0 cm (Jereb and Roper 2010).

Beaks of *P. margaritifera* were illustrated in Clarke (1986) and Lu and Ickeringill (2002). Neither flesh nor accumulated beaks of *P. margaritifera* were reported in any dietary studies of Southern Ocean predators.

***Stigmatoteuthis hoylei* (Goodrich, 1896) and *S. arcturi* Robson, 1948**: A cosmopolitan tropical and subtropical epi-meso-bathypelagic species complex, with *S. arcturi* being restricted to the Atlantic Ocean, while the closely-related *S. hoylei* occurs in the Indo-Pacific (Voss et al. 1998; Tolweb 2019). Nesis (1987) indicated that the species complex can reach subantarctic waters, but additional records and detailed information restrict its southern boundary to the STF (Voss et al. 1998). Hence, the occurrence of *S. hoylei* and *S. arcturi* within the Southern Ocean is doubtful. Mantle length to 24 and 20 cm for *S. hoylei* and *S. arcturi*, respectively (Voss et al. 1998).

The lower beaks of the three closely related species of the genus *Stigmatoteuthis* (Tolweb 2019) were not compared thoroughly, thus precluding identification at the species level.

However, their distinct geographical ranges allow giving a species name to the beaks collected in predators' stomach contents of the southern Atlantic (*S. arcturi*) and southern Indo-Pacific (*S. hoylei*). Beaks of *S. hoylei/arcturi* were well illustrated (Clarke 1980 Text-fig 192 and 193, 1986; Xavier and Cherel 2009). According to their morphological features, the lower beak of *Stigmatoteuthis* species belongs to the type A of histioteuthid beaks and corresponds to beak types A4 and A5 (Clarke 1980, 1986; YC unpublished data). It was sometimes not differentiated from other type A beaks (Rodhouse et al. 1987, 1990; Ridoux 1994; Green et al. 1998; Xavier et al. 2003b; Xavier and Croxall 2007). *Stigmatoteuthis* beaks were previously named *Histioteuthis dofleini* (Imber 1973, 1992, 1996; Berruti and Harcus 1978; Clarke 1980, 1986; Clarke et al. 1981; Imber and Berruti 1981; West and Imber 1986) and *Histioteuthis ?dofleini* (Imber and Russ 1975; Clarke and

Table 5 Biogeography and list of the 42 species of squids living within the Southern Ocean, including 21 endemics (in bold)

		Endemic		Species (alphabetical order)
Biogeography	*n*	*n*	%	
Circumpolar Antarctic (AZ)	1	**1**	**100.0**	***Psychroteuthis glacialis***
Circumpolar Southern Ocean	13	10	76.9	
AZ and PFZ	7	**7**	**100.0**	***Alluroteuthis antarcticus***
				Batoteuthis skolops
				Filippovia knipovitchi
				Galiteuthis glacialis
				Moroteuthopsis longimana
				***Psychroteuthis* sp. B**
				Slosarczykovia circumantarctica
AZ, PFZ and SAZ	6	**3**	**50.0**	***Asperoteuthis lui***
				Bathyteuthis abyssicola
				Chiroteuthis veranyi
				Gonatus antarcticus
				Mastigoteuthis psychrophila
				Mesonychoteuthis hamiltoni
Circumpolar subantarctic	20	7	35.0	
Regional subantarctic	8	3	37.5	
PFZ	1	**0**	**0.0**	*Promachoteuthis* sp. B
PFZ and SAZ	18	**7**	**38.9**	*Architeuthis dux*
				Brachioteuthis linkovskyi
				Gonatopsis octopedatus
				Histioteuthis atlantica
				Histioteuthis eltaninae
				Illex argentinus
				Liguriella podophtalma
				Martialia hyadesi
				Moroteuthopsis ingens
				***Moroteuthopsis* sp. B (Imber)**
				Nototeuthis dimegacotyle
				Onykia robsoni
				Pholidoteuthis massyae
				Taningia danae
				Taningia fimbria
				Taonius notalia
				Todarodes filippovae
				Todarodes* cf. *angolensis
SAZ	9	**3**	**33.3**	*Doryteuthis gahi*
				Enoploteuthis semilineata
				Galiteuthis suhmi
				Lycoteuthis lorigera
				Notonykia africanae
				Notonykia nesisi
				Nototodarus sloanii
				Octopoteuthis fenestra
				Ommastrephes cylindraceus
Occasional subantarctic	12	0	0.0	
Status unknown	1	0	0.0	

Abbreviations: *AZ* Antarctic Zone (south of the Polar Front), *PFZ* Polar Frontal Zone (between the Polar Front and the Subantarctic Front), *SAZ* Subantarctic Zone (between the Subantarctic Front and the Subtropical Front)

MacLeod 1982c; Schramm 1986). They were found as accumulated items in the diet of some Southern Ocean predators (e.g., Clarke 1980; Imber 1992; Xavier et al. 2014).

Brief synthesis

Fifty-four species of squids reliably occur within the Southern Ocean, including 12 species that were recorded occasionally (Tables 2 and 5). The 42 remaining squids belong to three large taxonomic units, namely bathyteuthoids ($n = 1$ species), myopsids ($n = 1$), and oegopsids ($n = 40$). A high level of endemism (21 species, 50%, all oegopsids) characterizes the Southern Ocean teuthofauna. Seventeen families of oegopsids are represented, with three families dominating the squid fauna (18 species, 45%), the onychoteuthids (seven species, five endemics), ommastrephids (six species, three endemics), and cranchiids (five species, three endemics) (Table 5). Two monotypic families are endemic to the Southern Ocean, the batoteuthid (*B. skolops*), and psychroteuthid (*P. glacialis*, but see below). Two taxa are only known from their beaks and therefore merit further investigations, the onychoteuthid *Moroteuthis* sp. B and the putative psychroteuthid *Psychroteuthis* sp. B.

Discussion

This review presents an innovative approach to investigate the teuthofauna from the Southern Ocean by combining and synthesizing for the first time two complementary data sets, firstly the conventional literature on cephalopod taxonomy and biogeography, and secondly the many dietary investigations conducted on subantarctic and Antarctic predators over the last 50 years. Overall, the review: (i) extends considerably the number of squid species, including endemics, recorded from the Southern Ocean; (ii) adds a lot of new records on poorly known and rare squids; (iii) provides new information on the previously understudied Southern Indian Ocean; (iv) completes the biogeography of many species, including squids that have a key role in the oceanic ecosystem; and finally (v) underlines the potential mismatch between nets and beaks, with predators catching larger specimens and a greater diversity of species than nets (Rodhouse 1990); for example, some rarely net-caught squids are common items in stomach contents (e.g., *B. skolops*). This innovative approach can be fruitfully applied to other marine areas where the diet of predators was heavily investigated over the last decades, as in the southern subtropical zone where many cephalopod eaters forage, e.g., sperm whales and large procellariform seabirds.

Table 6 Lists of species and of families of squids recorded within the Southern Ocean in previous investigations and in the present study. Occasional and doubtful records were excluded

	Species		Families	
	Total	Endemic	Total	Endemic
Worldwide review				
Nesis (1987)	34	17	18	1
Jereb and Roper (2010)	32	14	18	2
Southern Ocean review				
Xavier et al. (1999)	19	13	12	2
Rodhouse (2013)	18	12	12	2
Rodhouse et al. (2014)	19	12	12	2
Present study	42	21	19	2
Antarctic Zone review				
Lubimova (1985)	17	11	11	2
Filippova (2002)	16	12	12	2
Collins and Rodhouse (2006)	23	13	13	2
Xavier et al. (2018a)	20	14	13	2

The Southern Ocean and Antarctic Zone refer to water masses south of the Subtropical Front and south of the Polar Front, respectively (the AZ is the southern part of the Southern Ocean)

Comparison with previous reviews

Forty-two squids, including 21 endemics, live within the Southern Ocean (Table 5), thus increasing considerably the number of species listed in previous reviews focusing on the Southern Ocean teuthofauna (Table 6). This unexpected more than twofold increase results from a combination of (i) a previous incomplete checking of existing records (e.g., *A. dux, P. massyae, T. danae*), (ii) the non-inclusion of many subantarctic species (e.g., *I. argentinus, L. lorigera*, *N. sloanii*), (iii) the non-consideration of rare taxa (e.g., *L. podophtalma*, *Promachoteuthis* sp. B), and (iv) the non-consideration of information from predators' diet (e.g., *A. lui*, *N. dimegacotyle*). Overall, the first synthesis of cephalopods worldwide (Nesis 1987) was the most complete previous description of the Southern Ocean teuthofauna (Table 6), with the main limitation that improvement in squid taxonomy over the last 35 years added a few newly described species to the list (e.g., *B. linkovskyi*, *N. nesisi*, *O. fenestra*), and changed the names of many taxa (15 out of a total of 34 listed Southern Ocean species).

General comments

Worldwide biodiversity of cephalopods increases with decreasing latitudes, with more species (with low endemism) living in tropical and subtropical waters than in polar waters

(Nesis 2003). A recent study on oceanic pelagic cephalopods from the eastern Pacific demonstrated a major latitudinal distribution break at ~42°S, which matches with the location of the STF (the Southern Ocean northern limit), thus underlining the relative isolation of the Southern Ocean teuthofauna (Ibanez et al. 2019). The present review extends this pattern to the Southern Hemisphere overall, with only half of the 42 Southern Ocean species occurring both south and north of the STF (Table 5).

Four main features of the Southern Ocean teuthofauna emerge from the review. (i) The Southern Ocean is marked by the highest level of oceanic squid endemism (50%) in the world's oceans, with endemism increasing from north to south. Almost all species that live in the coldest waters are endemics, with the notable exceptions of *B. abyssicola*, *C. veranyi*, and *G. antarcticus* (Table 5). (ii) While previous works focused on the southern part of the Southern Ocean, the present review also highlights the importance of endemism in subantarctic waters. Ten squids are subantarctic endemics, including seven circumpolar species (*H. eltaninae*, *M. hyadesi*, *M. ingens*, *Moroteuthopsis* sp. B, *N. dimegacotyle*, *T. notalia*, and *Todarodes* cf. *angolensis*) and three regional endemics (*N. nesisi*, *N. sloanii*, and *O. fenestra*). The latter are restricted to the SAZ off Australasia (mainly New Zealand), a probable consequence of the long-term geological isolation of this island group that likely promoted speciation. (iii) Squid biodiversity within the Southern Ocean is at its minimum near the Antarctic shelf where less than ten squids were commonly caught by nets and/or predators (*A. antarcticus*, *B. abyssicola*, *G. glacialis*, *M. psychrophila*, *M. hamiltoni*, *M. longimana*, *P. glacialis*, and *S. circumantarctica*). By contrast, species richness is at its maximum within the PFZ where cold water squids co-exist with warmer-water subantarctic and subtropical species. This pattern of biodiversity is well illustrated by the contrasted cephalopod diet of the Patagonian toothfish that included 23–26 squid prey at the southern subantarctic Crozet and Kerguelen Islands, but only 13 squid species at the low-Antarctic South Georgia (Xavier et al. 2002b; Cherel et al. 2004). (iv) Indeed, the PF acts as the major Southern Ocean biogeographic barrier delimiting distinct squid assemblages within the Southern Ocean. This oceanic front is the main southern boundary of 19 squids, while 13 other species occur both south and north of it. Squid repartition is thus in agreement with the general view that the PF is a well-defined but not absolute barrier to large-scale distribution of marine organisms (Clarke et al. 2005). The SAF is also a significant barrier for squids, thus confirming its important role as a circumpolar zoogeographical boundary (Pakhomov et al. 2000). The SAF is the southern limit of nine warm-water squids and, notably, the northern limit of seven cold-water species, all endemics (Table 5).

Recent improvements in both taxonomy and beak identification illuminated some old problems and mismatches between nets and beaks, thus reconciliating the two complementary approaches. (i) For example, Nesis (1987, 2003) listed some cranchiids as having a subantarctic distribution, but the species were never identified in the diet of Southern Ocean predators until beaks previously determined under various names were assigned to *L. podophtalma* and *G. suhmi* (this study). (ii) In the same way, one of the most common unidentified food items of Southern Ocean predators was a *Taonius* beak, which corresponds to the recently described *T. notalia* (Evans 2018). (iii) Since the description of *Gonatus phoebetriae* from the examination of a single beak only (Imber 1978), the presence of a second species of gonatids within the Southern Ocean together with *G. antarcticus* was hotly debated (Kubodera and Okutani 1986; Nesis 1999; Tolweb 2019). The unexpected catch in 2007 of one specimen of *Gonatopsis octopedatus* south of the Falkland Islands (Arkhipkin et al. 2010) definitely added a second gonatid to the Southern Ocean teuthofauna. Subsequent examination of its beaks allowed synonymizing it with *G. phoebetriae*, thus, increasing significantly the number of records and detailing the repartition of *G. octopedatus* within the Southern Ocean (Table 3).

Predators and beaks

Identifying cephalopods from their beaks is always a challenge, but the resulting species determinations in dietary investigations improved considerably our knowledge on trophic relationships within the pelagic ecosystem of the Southern Ocean. Unfortunately, the species lists often included misidentifications and out-of-date species names, as underlined by a re-analysis of a subset of beaks from regurgitated casts of albatrosses from Marion Island (Imber and Berruti 1981). Amongst the 42 different cephalopod taxa that were initially identified, one (2.4%) beak was not found in the collection, the labeling of 14 (33.3%) beaks was right, but the name of the 27 (64.3%) remaining taxa had to be changed due to misidentifications ($n = 11$, 26.2%) and to improvement in both beak identification ($n = 8$, 19.0%) and taxonomy ($n = 8$, 19.0%) (Table 7). Consequently, many pioneer dietary investigations are now either impossible (e.g., Imber 1973) or difficult (e.g., Rodhouse et al. 1987; Ridoux 1994) to interpret, including the seminal work by Clarke (1980) on the cephalopod prey of sperm whales. Hence, great care is needed when using data from old studies conducted in the 70s and 80s when identification was still at its beginning. The present review helps to disentangle synonymies and misidentifications of most squids, but some beaks were not examined by the author, including doubtful identifications (e.g., *Liocranchia* sp.; Slip 1995; Slip et al. 1995; van den Hoff 2004) and unidentified beaks from notoriously difficult taxa (e.g., *Mastigoteuthis* spp. in many studies).

Table 7 Improvement in cephalopod identification and taxonomy over time: the re-analysis and update of the cephalopod prey of albatrosses from Marion Island (Imber and Berruti 1981)

	This study	Imber and Berruti (1981)	Comments
Oegopsida			
Ancistrocheiridae	*Ancistrocheirus lesueurii*	*Ancistrocheirus lesueuri*	No change
Architeuthidae	*Architeuthis dux*	*Architeuthis* sp.	New species name (taxonomic improvement)
Batoteuthidae	*Batoteuthis skolops*	*Chiroteuthis* sp. E	New name (identification improvement)
Chiroteuthidae	*Asperoteuthis lui*	*Chiroteuthis macrosoma*	New name (identification improvement)
	Chiroteuthis joubini	*Chiroteuthis veranyi*	New species name (misidentification)
	Chiroteuthis veranyi	*Chiroteuthis picteti*	New species name (misidentification)
Cranchiidae	*Galiteuthis glacialis*	*Teuthowenia antarctica*	New name (misidentification)
	Galiteuthis suhmi	*Megalocranchia maxima*	New name (misidentification)
	Liguriella podophtalma	*Taonius belone*	New name (misidentification)
	Mesonychoteuthis hamiltoni	*Mesonychoteuthis hamiltoni*	No change
	Taonius notalia	*Taonius cymoctypus*	New species name (identification and taxonomic improvement)
	Taonius expolitus	*Taonius pavo*	New species name (identification and taxonomic improvement)
	Teuthowenia pellucida	*Teuthowenia megalops impennis*	New species name (misidentification)
Cycloteuthidae	*Cycloteuthis sirventi*	*Cycloteuthis sirventi*	No change
	Discoteuthis discus	*Discoteuthis discus*	No change
	unknown oegopsid	*Discoteuthis* sp. C	Beak not examined
Gonatidae	*Gonatopsis octopedatus*	*Gonatus phoebetriae*	New name (identification improvement)
	Gonatus antarcticus	*Gonatus antarcticus*	No change
Histioteuthidae	*Histioteuthis atlantica*	*Histioteuthis atlantica*	No change
	Histioteuthis bonnellii corpuscula	*Histioteuthis meleagroteuthis*	New species name (misidentification)
	Histioteuthis eltaninae	*Histioteuthis eltaninae*	No change
	Histioteuthis macrohista	*Histioteuthis macrohista*	No change
	Histioteuthis meleagroteuthis	*Histioteuthis? bruuni*	New species name (taxonomic improvement)
	Histioteuthis miranda	*Histioteuthis miranda*	No change
	Stigmatoteuthis hoylei/arcturi	*Histioteuthis dofleini*	New name (taxonomic improvement)
Mastigoteuthidae	*Mastigoteuthis psychrophila*	*Mastigoteuthis* sp. C	New species name (identification improvement)
	Magnoteuthis osheai	*Mastigoteuthis* sp. A	New name (identification improvement)
Neoteuthidae	*Alluroteuthis antarcticus*	*Galiteuthis glacialis, Bathothauma lyromma*	New name (misidentifications)
	Nototeuthis dimegacotyle	*Galiteuthis armata*	New name (misidentification)
Octopoteuthidae	*Octopoteuthis* sp.	*Octopoteuthis* sp.	No change
	Taningia danae	*Taningia danae*	No change (but see text)
Ommastrephidae	*Martialia hyadesi*	*Martialia hyadesi*	No change
	Todarodes filippovae	*Nototodarus* sp.	New name (genus *Nototodarus* does not occur in the area)
Onychoteuthidae	*Filippovia knipovitchi*	*Moroteuthis knipovitchi*	New genus name (taxonomic improvement)
	Moroteuthopsis ingens	*Moroteuthis ingens*	New genus name (taxonomic improvement)
	Moroteuthopsis longimana	*Kondakovia longimana*	New genus name (taxonomic improvement)
	Moroteuthopsis sp. B	Undescribed gen. & sp.	New name (well-known beak from an unknown onychoteuthid)
	Onykia robsoni	*Moroteuthis robsoni*	New genus name (taxonomic improvement)
Psychroteuthidae	*Psychroteuthis glacialis*	*Psychroteuthis glacialis*	No change
	Psychroteuthis sp. B	*Psychroteuthis* sp. B	Well-known beak from an unknown squid
Incirrata			
Alloposidae	*Haliphron atlanticus*	*Alloposus mollis*	New name (taxonomic improvement)

Beaks were examined at the Port Elizabeth Museum at Bayworld in September 2018

The thorough examination of beaks from holotypes, paratypes, and other specimens improved significantly beak identification over recent years (e.g., *A. lui*, *T. notalia*), thus reducing to only two the number of well-described beaks (*Moroteuthopsis* sp. B and *Psychroteuthis* sp. B) from still unknown squids living in subantarctic and Antarctic waters. The taxonomic status of *Psychroteuthis* sp. B remains to be determined, being a small form of *P. glacialis*, another *Psychroteuthis* species, or a new species not related to *Psychroteuthis*. By contrast, the status of *Moroteuthopsis* sp. B is well defined as a still unknown onychoteuthid. The best way to describe the species is probably to sort beaks and collect DNA samples from every caught Southern Ocean onychoteuthids and especially from those looking like some well-known and commonly-caught species (e.g., *M. ingens*).

Conclusion and perspective

Due to the considerable body of literature on Southern Ocean squids and to the large amounts of beaks that were identified from stomach contents over the last decades, it is likely that all the most common squid species inhabiting the Southern Ocean are now well described (but *Moroteuthopsis* sp. B, *Psychroteuthis* sp. B), including every species that are ecologically relevant (but *Todarodes* cf. *angolensis*). This does not preclude the finding of either new cryptic forms within species complexes using DNA analysis (e.g., *H. atlantica*, *O. robsoni*) or the discovery of a few new species in the deep-sea or in the most remote regions of the Southern Ocean.

The next promising step to gather new information on the biology of Southern Ocean squids relies in their underwater observations using submersibles and related in situ mechanisms, as baited vertical longlines (Kubodera and Mori 2005), towed platforms (Hoving et al. 2019), remote-operated vehicles (Hoving et al. 2013), and manned submersibles (Harrop et al. 2014). Bio-logging is another complementary option and the continuous development of efficient miniaturized electronic devices allows today using camera-bearing animals in the epi- and mesopelagic, e.g., diving seabirds (Pistorius et al. 2020) and marine mammals (Aoki et al. 2015). Their species richness in terms of both cephalopod species and top predators make slope waters surrounding subantarctic islands the ideal geographical hotspots to investigate the Southern Ocean teuthaufauna, with the challenge that the materials should be deployed within the roaring 40s and furious 50s.

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Compliance with ethical standards

Conflict of interest The author declares that he has no conflict of interest.

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